The Lichenologist **41**(6): 571–604 (2009)
doi:10.1017/S0024282909008317

The taxonomy of the *Caloplaca citrina* group (*Teloschistaceae*) in the Black Sea region; with contributions to the cryptic species concept in lichenology

Jan VONDRÁK, Pavel ŘÍHA, Ulf ARUP and Ulrik SØCHTING

Abstract: A new taxonomy of the *Caloplaca citrina* group in the Black Sea region is presented. It is based on the nrDNA ITS molecular data, chemistry (anthraquinone contents) and 20 morphological characters. Six species previously known in the region are accepted: *Caloplaca arcis*, *C. calcitrapa*, *C. dichroa*, *C. flavocitrina*, *C. geleverjae*, *C. limonia*. Five new species are described: *Caloplaca arcisproxima*, *C. austrocitrina*, *C. communis*, *C. confusa* and *C. nigromarina*. Seven further species, *Caloplaca britannica*, *C. citrina*, *C. marina*, *C. maritima*, *C. microthallina*, *C. ora* and *C. phlogina* are also treated briefly. Some maritime species known from the Atlantic coast of Europe are absent from the region, and, surprisingly, *Caloplaca citrina* s. str. could not be confirmed from the study area. A key to the species present in the region is provided, although morphological characters are of very limited value in this group. The variability and taxonomic importance of particular features are discussed. No significant differences in secondary chemistry were observed among the species.

Many examples of convergence and some semi-cryptic species were revealed by molecular data. The term 'semi-cryptic species' is introduced here into lichenology for those species which cannot be clearly diagnosed by their morphology, but which are determined by other characters, mainly by their ecology and distribution. We propose to describe formally such species, in spite of difficulties with subsequent morphological identification.

Key words: alveolate cortex, *Caloplaca citrina* clade, lichens, nrDNA ITS, semi-cryptic species, *Teloschistales*

Introduction

A number of lichenological papers, dealing with taxonomy or biodiversity, have included lichen species inhabiting seashore habitats but only some of these have dealt with particular taxonomic groups occurring specifically on coastal cliffs, e.g. *Ramalina* in Sheard (1978), *Roccella* in Tehler *et al.* (2004), *Verrucaria* in for example Brodo & Santesson (1997), Harada (2004) or McCarthy (1991), and *Xanthoria* in Lindblom & Ekman (2005). Marine and maritime lichens are well-known in some regions, for instance in the British Isles, where some ecological and generalized studies have been made (e.g. Fletcher 1973*a*,*b*, 1975*a*,*b*). The genus *Caloplaca* has been intensively investigated on North American shores (Arup 1992*a*,*b*, 1993*a*,*b*, 1994, 1995*a*,*b*, 1997*b*) and in Europe (e.g. Tavares 1956; Laundon 1992; Roux & Navarro-Rosinés 1992; Navarro-Rosinés & Roux 1993, 1995; Arup 1997*a*). In the East Mediterranean and the Black Sea region, some papers, mainly contributions on lichen biodiversity, partially cover maritime species, including *Caloplaca* (e.g. Szatala 1943*a*, *b*; Vězda 1975; Roux & Navarro-Rosinés 1992; Güvenc & Öztürk 1999; Sipman & Raus 1999, 2002; Yazici 1999; Khodosovtsev 2001, 2002, 2003; Redchenko

J. Vondrák: Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, České Budějovice, CZ-370 05, Czech Republic. Email: j.vondrak@seznam.cz
P. Říha: Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 31, České Budějovice, CZ-370 05, Czech Republic.
U. Arup: Botanical Museum, Lund Univeristy, Östra Vallgatan 18, SE-223 61 Lund, Sweden.
U. Søchting: Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Ø. Farimagsgade 2D, DK-1353 Copenhagen, Denmark.

2002; Khodosovtsev *et al.* 2003, 2007; John & Breuss 2004; Sipman *et al.* 2005; Vondrák & Slavíková-Bayerová 2006; Vondrák *et al.* 2008*a*;), but otherwise knowledge of maritime species of this area remains sparse.

While working in the Black Sea region, one of us (JV) found that current W European literature for the identification of lichens (species in the genera *Caloplaca*, *Candelariella*, *Catillaria*, *Lecania* and *Toninia*) was inadequate. This was particularly true for the genus *Caloplaca*, which appeared to be extremely species-rich in the area. Currently, we estimate that more than 50 species occur in coastal habitats around the Black Sea. This huge, but largely unknown diversity, led us to initiate a complex project on the biodiversity of the genus *Caloplaca* in the Black Sea region and the present study focuses on the taxonomy of the *Caloplaca citrina* group in the area. Arup (2006*a*) has already clarified the taxonomy of this group in Scandinavia and his results are utilized and developed further here. This group seems to be rather species rich and according to phylogenetic studies it is closely related to the *C. saxicola* group, various clades of *Xanthoria* species and the *C. holocarpa* group (Arup & Grube 1999; Gaya *et al.* 2008).This paper describes the species diversity in the *C. citrina* group.

The taxonomy proposed in this study is based on molecular data using the single locus, ITS nrDNA. This locus is usually well suited for taxonomic studies at the species level, and a number of published papers using only this region has given meaningful results in the genus *Caloplaca* (Tretiach *et al.* 2003; Arup 2006*a*, 2009; Arup *et al.* 2007; Søchting & Figueras 2007; Muggia *et al.* 2008; Vondrák *et al.* 2008*b*,*c*). The only study in *Teloschistaceae* so far using a multilocus approach is one dealing with taxonomy at higher than species level (Søchting & Lutzoni 2003). Our investigations have some general implications exceeding the framework of a regional taxonomic study since the molecular results have revealed several distinct groups, which are often morphologically hardly distinguishable. This phenomenon, termed semi-cryptic speciation, is discussed at the end of the paper.

Material and Methods

Material from the Atlantic coast of Europe used for comparison (mainly of *Caloplaca britannica*, *C. littorea*, *C. marina*, *C. maritima*, and *C. microthallina*) was obtained on loan from BM, CBFS, LD, and hb. A. Aptroot (ABL). Material from Central Europe, the Black Sea region and the Mediterranean was obtained on loan from B, BP, CBFS, GZU, KHER, PRM, SAV and W. The main part of the material from the Black Sea region was collected by the first author during field excursions in July 2004 (Bulgaria), July and November 2005 (Romania, Bulgaria, European part of Turkey), June 2006 (Ukraine: Crimea), and April, May 2007 (Romania, Bulgaria, Turkey, Georgia, Russia, Ukraine). Vouchers are deposited in CBFS (the numbers following this abbreviation are herbarium accession numbers).

Citations of specimens examined are abbreviated and for common species only selected specimens are presented. Data on additional samples and full sample information are available on the web page: http://botanika.bf.jcu.cz/lichenology/data.php.

Morphology and anatomy

A total of 20 characters was measured and used in the detailed characterization of the *Caloplaca citrina* group, but only 11 traits were important for species separation: width of areoles, thickness of thallus and cortex/alveolate cortex, size of vegetative diaspores, size of apothecia, exciple width, hymenium height, size of ascospores, width of spore septa, width of paraphyses tips and size of conidia.

Sections for morphological examination were cut by hand and observed in water, but paraphysis tips and cortical tissues were observed after pretreatment with KOH. Measurements were made to an accuracy of 0·5 μm for cells (e.g. ascospores, conidia and paraphyses), 1 μm for thickness of the cortex and 10 μm for larger structures (e.g. hymenium thickness and exciple width). All measurements of cells included their walls. Measurements are given as (min.–) $x \pm$ SD (–max.), where x = mean value and SD = standard deviation. The total numbers of measurements (n) are given in parentheses. At least five measurements were taken from all specimens available; in the morphologically indistinguishable species (*Caloplaca confusa*, *C. nigromarina*), only specimens confirmed by molecular data were used for measurements.

Morphological terminology follows Ryan *et al.* (2002) and Bungartz (2002). The term 'alveolate cortex' is proposed here for a hyaline tissue formed by living fungal cells among dead algal cells or in gaps left by dead algal cells. It is similar to a phenocortex (*sensu* Ryan *et al.* 2002: 23), but differs in fungal cells, which are living, and not dead as in a phenocortex. Being situated between algal and epinecral layers, it replaces a true cortex in some species.

DNA extraction and amplification.

Direct PCR was used for DNA extraction and PCR-amplification of the nuclear ITS regions including the

TABLE 1. *Voucher specimens and GenBank accession numbers of the ITS sequences used in the phylogenetic analysis. Accession numbers in bold represent new sequences produced during this study*

Species & Herbarium Accession No.	Source	GenBank Accession No.
Caloplaca arcis	Austria. (Arup 2006*a*)	DQ173213
C. arcis	Sweden. (Arup 2006*a*)	DQ173214
C. arcis	Great Britain, England. (Arup 2006*a*)	DQ173215
C. arcis W1990-00525	Italy, Sardinia (coll. *W. Brunnbauer* 1986)	**EU563454**
C. arcis CBFS JV3036	Bulgaria, Black Sea coast (coll. *Vondrák* 2005)	**EU563395**
C. arcis CBFS JV4985	The Netherlands, Noordoostpolder (coll. *A. Aptroot* 59871, 2004)	**EU563453**
C. arcis CBFS JV4986	The Netherlands, Gelderland (coll. *A. Aptroot* 59582, 2003)	**EU563452**
C. arcis CBFS JV5426	Turkey, Black Sea coast (coll. *Vondrák* 2007)	**EU563424**
C. arcis CBFS JV6093	Bulgaria, Black Sea coast (coll. *Vondrák* 2007)	**EU563438**
C. arcisproxima CBFS JV4125	Greece, South Crete (coll. *Vondrák* 2005)	**EU563413**
C. arcisproxima CBFS JV5473	Ukraine, Black Sea coast (coll. *Vondrák* 2007)	**EU563425**
C. austrocitrina CBFS JV991	Czech Republic, České Budějovice (coll. *Vondrák* 2003)	**EU563450**
C. austrocitrina CBFS JV3436	Romania, Black Sea coast (coll. *Vondrák* 2005)	**EU563406**
C. austrocitrina CBFS JV4195	Greece, North Crete (coll. *Vondrák* 2005)	**EU563416**
C. austrocitrina CBFS JV4631	Bulgaria, Black Sea coast (coll. *Vondrák* 2005)	**EU563417**
C. austrocitrina CBFS JV5236	Ukraine, Black Sea coast (coll. *Vondrák* 2006)	**EU563419**
C. austrocitrina CBFS JV5285	Ukraine, Black Sea coast (coll. *Vondrák* 2006)	**EU563420**
C. austrocitrina CBFS JV5474	Russia, Black Sea coast (coll. *Vondrák* 2007)	**EU563426**
C. austrocitrina CBFS JV5476	Ukraine, Black Sea coast (coll. *Vondrák* 2007)	**EU563427**
C. austrocitrina CBFS JV6097	Russia, Black Sea coast (coll. *Vondrák* 2007)	**EU563441**
C. calcitrapa	France, Languedoc-Roussellon, isotype (Arup 2006*a*)	DQ173227
C. calcitrapa CBFS JV3408	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563401**
C. calcitrapa CBFS JV5486	Bulgaria, Black Sea coast (coll. *Vondrák* 2007)	**EU563431**
C. calcitrapa CBFS JV6100	Turkey, Marmara Sea coast (coll. *Vondrák* 2007)	**EU563444**
C. citrina	Sweden. (Arup 2006*a*)	DQ173222
C. citrina	Sweden. (Arup 2006*a*)	DQ173223
C. citrina	Sweden. (Arup 2006*a*)	DQ173224
C. citrina	Sweden. (Arup 2006*a*)	DQ173225
C. citrina	Sweden. (Arup 2006*a*)	DQ173226
C. citrina CBFS JV1138	Czech Republic, Andělská Hora (coll. *Vondrák* 2003)	**EU563387**
C. communis CBFS JV3471	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563409**
C. communis CBFS JV3042	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563397**
C. communis CBFS JV3037	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563396**
C. communis CBFS JV3367	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563399**
C. communis CBFS JV3763	Greece, South Crete (coll. *Vondrák* 2005)	**EU563410**
C. communis CBFS JV3803	Greece, North Crete (coll. *Vondrák* 2005)	**EU563411**
C. communis CBFS JV5481	Turkey, Gallipoli Peninsula (coll. *Vondrák* 2007)	**EU563429**
C. communis CBFS JV6092	Turkey, Gallipoli Peninsula (coll. *Vondrák* 2007)	**EU563437**
C. communis CBFS JV6104	Russia, Taman Peninsula, Sea of Azov coast (coll. *Vondrák* 2007)	**EU563446**
C. communis CBFS JV6113	Bulgaria, Black Sea coast (coll. *Vondrák* 2007)	**EU563447**
C. communis CBFS JV6119	Turkey, Black Sea coast (coll. *Vondrák* 2007)	**EU563448**
C. confusa CBFS JV3435	Bulgaria, Black Sea coast (coll. *Vondrák* 2005)	**EU563405**
C. confusa CBFS JV6206	Bulgaria, Black Sea coast (coll. *Vondrák* 2007)	**EU563449**
C. confusa herb. F. Berger	Azores, Sao Jorje (coll. *F. Berger* 1992)	**EU563468**
C. confusa GZU Haf31862	France, Corsica (coll. *J. Hafellner* 1993)	**EU563457**
C. confusa GZU	Italy, Sicily (coll. *J. Poelt* 1992)	**EU563455**
C. dichroa	Sweden. (Arup 2006*a*)	DQ173228
C. dichroa	Sweden. (Arup 2006*a*)	DQ173229
C. dichroa	Sweden. (Arup 2006*a*)	DQ173230

TABLE 1. *Continued*

Species & Herbarium Accession No.	Source	GenBank Accession No.
C. dichroa	Sweden. (Arup 2006*a*)	DQ173231
C. dichroa	Sweden. (Arup 2006*a*)	DQ173232
C. dichroa CBFS JV5324	Romania, Black Sea coast (coll. *Vondrák* 2007)	**EU563421**
C. dichroa CBFS JV5477	Ukraine, Karadag (coll. *Vondrák* 2007)	**EU563428**
C. dichroa CBFS JV4155	Great Britain, England (coll. *Vondrák* 2006)	**EU563415**
C. dichroa GZU Haf43519	Austria, Tirolia, alt. *c.* 1000 m (coll. *J. Hafellner* 1997)	**EU563458**
C. flavocitrina	Sweden. (Arup 2006*a*)	DQ173216
C. flavocitrina	Sweden. (Arup 2006*a*)	DQ173217
C. flavocitrina	Sweden. (Arup 2006*a*)	DQ173218
C. flavocitrina	Sweden. (Arup 2006*a*)	DQ173219
C. flavocitrina	Sweden. (Arup 2006*a*)	DQ173220
C. flavocitrina	Austria. (Arup 2006*a*)	DQ173221
C. flavocitrina CBFS JV1495	Czech Republic, Husinec (coll. *Vondrák* 2002)	**EU563388**
C. flavocitrina CBFS JV2106	Bulgaria, Black Sea coast, epiphytic (coll. *Vondrák* 2004)	**EU563390**
C. flavocitrina CBFS JV2536	Czech Republic, Kalubice (coll. *Vondrák* 2005)	**EU563392**
C. flavocitrina CBFS JV3425	Bulgaria, Black Sea coast, concrete (coll. *Vondrák* 2005)	**EU563404**
C. flavocitrina CBFS JV6089	Russia, Black Sea coast (coll. *Vondrák* 2007)	**EU563434**
C. flavocitrina CBFS JV6090	Turkey, Black Sea coast (coll. *Vondrák* 2007)	**EU563435**
C. flavocitrina CBFS JV6094	Georgia, Shuakhevi (coll. *Vondrák* 2007)	**EU563439**
C. flavocitrina CBFS JV6095	Russia, Black Sea coast (coll. *Vondrák* 2007)	**EU563440**
C. flavocitrina CBFS JV6098	Georgia, Black Sea coast (coll. *Vondrák* 2007)	**EU563442**
C. flavocitrina GZU Haf31888	Italy, Livorno, coastal rock (coll. *J. Hafellner* 1993)	**EU563456**
C. flavocitrina GZU Wetm76242	Hawaii, alt. c. 1700 m (coll. *C. Wetmore* 1996)	**EU563471**
C. geleverjae CBFS JV5415	Ukraine, Black Sea coast, topotype (coll. *Vondrák* 2007)	**EU563423**
C. havaasii BG	Norway, topotype (Arup 2006*b*)	DQ647649
C. limonia GZU	Italy, Marettimo, paratype (coll. *Poelt* 1991)	**EU563467**
C. limonia CBFS JV2515	Czech Republic, Písek (coll. *Vondrák* 2005)	**EU563391**
C. limonia CBFS JV3388	Bulgaria, Black Sea coast (coll. *Vondrák* 2005)	**EU563400**
C. limonia CBFS JV3410	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563402**
C. limonia CBFS JV3413	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563403**
C. limonia CBFS JV3438	Bulgaria, Black Sea coast (coll. *Vondrák* 2005)	**EU563407**
C. limonia CBFS JV3465	Bulgaria, Black Sea coast (coll. *Vondrák* 2005)	**EU563408**
C. limonia CBFS JV5352	Romania, Black Sea coast (coll. *Vondrák* 2007)	**EU563422**
C. limonia CBFS JV6101	Turkey, Black Sea coast (coll. *Vondrák* 2007)	**EU563445**
C. marina	Great Britain, England (Arup & Grube 1999)	AF353946
C. marina	North America, western coast (Arup & Grube 1999)	AF353947
C. marina BM 730882	Great Britain, Wales (2004)	**EU563461**
C. marina C US7520	Iceland, S-Múlasýla (coll. *U. Søchting* 1997)	**EU563470**
C. maritima	Great Britain, Wales (Arup & Grube 1999)	AF353948
C. maritima CBFS JV4943	Great Britain, Wales (coll. *U. Arup* L92256, 1992)	**EU563462**
C. maritima CBFS JV4987	The Netherlands, Walcheren (coll. *A. Aptroot* 59408, 2003)	**EU563451**
C. microthallina C US7480	Sweden, Halland (coll. *U. Søchting* 1997)	**EU563469**
C. microthallina CBFS JV4939	Great Britain, England (coll. *U. Arup* L92274, 1992)	**EU563464**
C. microthallina CBFS JV4940	Great Britain, England (coll. *U. Arup* L92291, 1992)	**EU563463**
C. microthallina CBFS JV4941	Great Britain, Wales (coll. *U. Arup* L92307, 1992)	**EU563465**
C. nigromarina GZU Lich.Anat. Exsic. 80	Turkey, Black Sea coast (coll. *V. John & E. Sauer* 1992)	**EU563459**
C. nigromarina CBFS JV3035a	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563393**
C. nigromarina CBFS JV3035b	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563394**
C. nigromarina CBFS JV3354	Turkey, Black Sea coast (coll. *Vondrák* 2005)	**EU563398**
C. nigromarina CBFS JV5482	Turkey, Gallipoli Peninsula (coll. *Vondrák* 2007)	**EU563430**
C. nigromarina CBFS JV4983	Bulgaria, Black Sea coast (coll. *Vondrák* 2004)	**EU563418**

TABLE 1. *Continued*

Species & Herbarium Accession No.	Source	GenBank Accession No.
C. nigromarina CBFS JV6091	Georgia, Black Sea coast (coll. *Vondrák* 2007)	**EU563436**
Caloplaca cf. *ora* CBFS JV3836	Greece, North Crete (coll. *Vondrák* 2005)	**EU563412**
C. phlogina CBFS JV3437	Romania, Black Sea coast (coll. *Vondrák* 2005)	**EU563460**
Caloplaca sp. CBFS JV4146	Greece, South Crete (coll. *Vondrák* 2005)	**EU563414**
Caloplaca sp. CBFS JV6086	Turkey, Black Sea coast (coll. *Vondrák* 2007)	**EU563433**
Caloplaca sp. CBFS JV2051	Bulgaria, Lyubimets (coll. *Vondrák* 2004)	**EU563389**

5.8S region of the nuclear ribosomal DNA gene (abbreviated as ITS) following Arup (2006*a*). Primers for amplification were ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). PCR cycling parameters followed Ekman (2001).

Phylogenetic analyses

The ITS sequences used in the phylogenetic analysis are listed in Table 1. *Caloplaca holocarpa* was used as the outgroup. The alignment was conducted using MAFFT 6 (on-line version in the Q-INS-i mode; see Katoh *et al.* 2002) and manually trimmed in BioEdit 7.0 (Hall 1999) to eliminate the unalignable ends.

Bayesian phylogenetic analysis was carried out with a Metropolis-coupled Markov chain Monte Carlo (MCMCMC) algorithm (Altekar *et al.* 2004) implemented in MrBayes 3.0 (Ronquist and Huelsenbeck 2003). Prior to the analysis, Mr Modeltest 2.2 (Nylander *et al.* 2004) was employed to assign the best-fit likelihood settings according to the hLRT (likelihood ratio test). The general time reversible model with some invariable sites (GTR+I+Γ) was determined as the best-fitting. A flat Dirichlet prior distribution with all values set to 1·0 was used to model the prior probability densities of the substitution rates as well as the stationary nucleotide frequencies. In order to assess the stability of the MCMC process, we monitored the standard deviation of split frequencies of two simultaneous independent runs, each including six parallel chains (one 'cold' and five incrementally heated by a temperature of 0·3). Every 100th count of the total of 5 000 000 generations for each run was sampled and the first quarter of samples was discarded as burn-in. The resulting 75 000 trees were used for reconstruction of a 50% majority-rule consensus tree.

The heuristic parsimony search was conducted in PAUP 4.0b10 (Swofford 2002), assessing the credibility of branches via non-parametric bootstrapping. In order to reduce the computational demands, a two-level analysis was chosen: the treespace was examined during the first run using the `nChuck=3 chuckScore=1` option for 100 replicates of the random sequence addition. The second search was performed on the stored trees and filled up the treespace thanks to the option `nChuck=0 chuckScore=0`. The maximum number of trees in memory was restricted to 250 000 using the `maxTrees` option. Bootstrap analysis encompassed 1000 resamplings and proceeded similar to the heuristic parsimony search with the exception of `nChuck` setting (=10) and number of RAS (=10) during the first run of analysis. The TBR algorithm was employed, all characters were equally weighted and the gaps were treated as missing data. The steepest descent option was not in effect and the analysis ran under the `mulTrees` option.

Chemistry

The acetone extracts of anthraquinones were subjected to high-performance liquid chromatography (HPLC) analysis. Reverse phase column (C18, 5µm, Lichrocart 250-4) was eluted with MeOH / 30%MeOH + 1%H_3PO_4 for 77 min and the absorbances at 270 nm were recorded (for details see Søchting 1997). The compounds were determined on the basis of their retention times and absorption spectra; samples examined are listed in Table 2.

Results and Discussion

Phylogeny

We confined the '*Caloplaca citrina* clade' to a group of morphologically variable species, to which we found *C. holocarpa* as closest outgroup (Fig. 1). According to Gaya *et al.* (2008), *Caloplaca granulosa* is a closer relative to the '*Caloplaca citrina* clade', but it is probably too close to the ingroup or may even belong within it. In fact, our circumscription of the '*Caloplaca citrina* clade' was made arbitrarily to cover the majority of taxa with the '*Caloplaca citrina* morphology' (see Morphology below) in the Black Sea region.

The resulting dataset contained 105 terminals assigned to 20 species, of which 17 are named here. The alignment had 674 positions, of which 233 were variable and 112 were parsimony informative. The first run of

TABLE 2. *Anthraquinone contents (% concentrations) of selected species in the* Caloplaca citrina *clade*

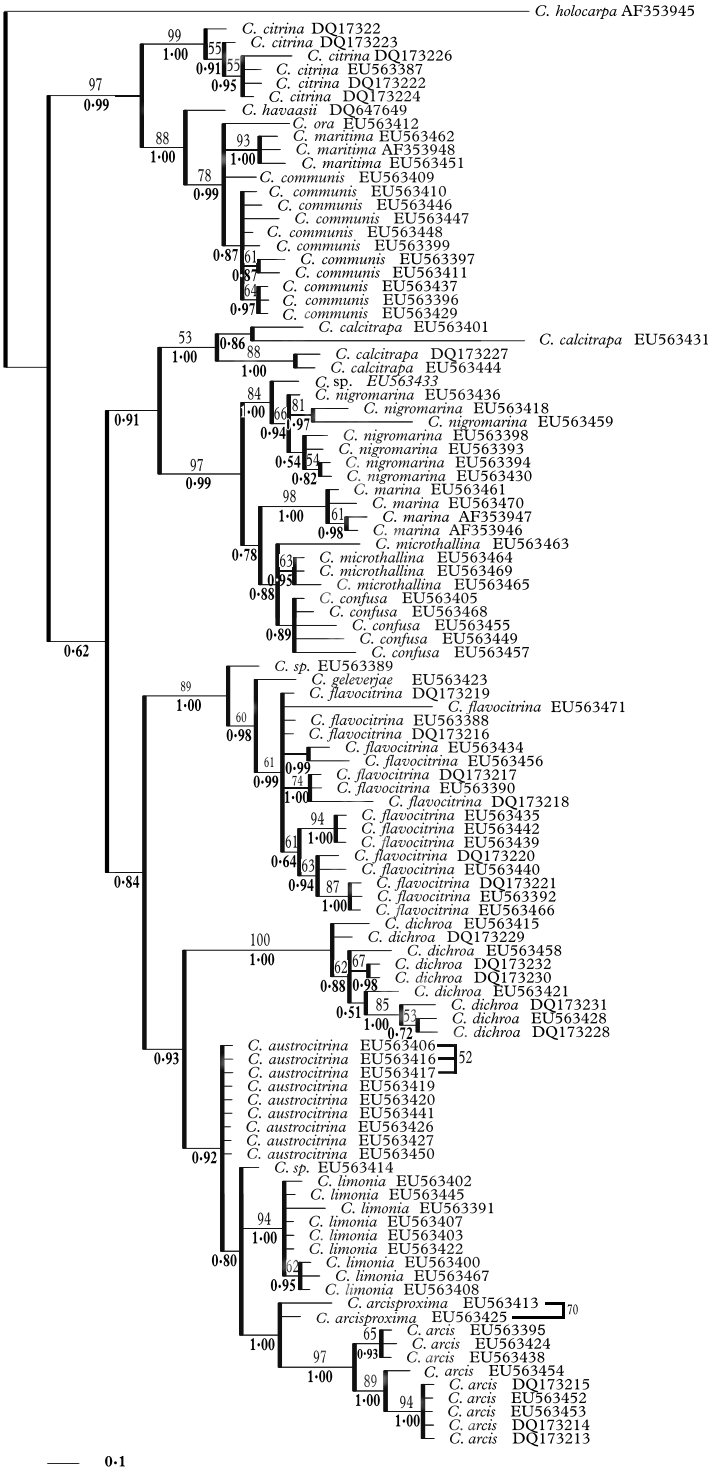
	teloschistin	falacinal	parietinic acid	emodin	parietin
C. arcis					
CBFS JV3036 (AP)	0·6	2·3	1·1	1·0	93·9
CBFS JV3036 (TH)	1·0	8·1	1·0	0·7	89·3
CBFS JV5426 (AP)	1·0	7·5	1·4	0·4	88·8
C. austrocitrina					
CBFS JV991 (TH)	1·4	5·4	0·0	1·0	92·2
CBFS JV4195 (AP)	3·3	16·8	2·1	1·3	76·5
CBFS JV4195 (TH)	3·4	26·7	1·3	1·5	67·1
CBFS JV5474 (AP)	2·3	14·1	1·6	0·8	80·1
C. calcitrapa					
CBFS JV3408 (AP)	0·6	2·0	0·7	0·8	96·0
C. citrina s.str.					
CBFS JV1138 (AP)	0·6	1·6	0·6	0·7	96·5
C. communis					
CBFS JV3367 (AP)	0·7	1·6	0·9	0·8	96·0
CBFS JV3367 (TH)	1·4	2·1	0·0	2·1	94·4
CBFS JV3467 (AP)	2·0	4·6	1·1	0·7	91·6
CBFS JV3763 (AP)	2·2	6·2	1·9	0·8	88·6
CBFS JV3803 (AP)	2·3	4·1	1·3	0·6	91·5
CBFS JV4114 (AP)	4·6	6·7	1·7	0·5	86·5
C. confusa					
CBFS JV3435 (TH)	1·2	3·8	1·0	1·0	93·0
C. dichroa					
CBFS JV5337 (AP)	1·2	2·5	1·0	1·1	94·3
CBFS JV5337 (TH)	0·6	4·1	0·7	0·6	93·9
C. flavocitrina					
CBFS JV3425 (AP)	5·3	12·1	1·4	0·7	80·4
CBFS JV3425 (TH)	1·5	9·6	0·0	0·0	88·8
C geleverjae					
CBFS JV5415 (AP)	1·1	2·2	0·6	1·4	94·7
C. limonia					
CBFS JV2515 (AP)	0·4	1·2	0·5	0·5	96·3
CBFS JV2515 (TH)	0·4	1·0	0·0	0·7	95·0
CBFS JV3388 (AP)	0·5	2·4	0·6	0·6	95·9
CBFS JV3388 (TH)	0·9	2·9	1·4	1·9	92·9
CBFS JV3438 (AP)	0·9	3·0	1·7	0·9	93·4
CBFS JV3465 (AP)	0·5	1·8	0·8	0·8	96·0
C. nigromarina					
CBFS JV3035 (TH)	1·2	9·4	0·9	0·7	87·8
CBFS JV3354 (TH)	1·4	2·5	0·3	0·7	95·1
CBFS JV3399 (TH)	1·6	13·6	0·5	0·5	83·7
CBFS JV3478 (TH)	1·4	6·2	0·7	0·8	90·9
GZU, *Lich. Anatol. Exs.* 80 (AP)	1·4	5·9	2·0	1·1	89·7
GZU, *Lich. Anatol. Exs.* 80 (TH)	2·2	12·8	0·0	0·	85·0
C. ora					
GZU, isotype (AP)	0·7	1·9	0·8	0·6	96·0
GZU, isotype (TH)	0·0	0·0	0·0	0·9	99·1
GZU, A. Vězda: *Lich. Rar. Esc.* 34 (AP)	0·4	1·3	0·9	0·4	97·0
GZU, A. Vězda: *Lich. Rar. Exs.* 34 (TH)	0·4	1·3	0·7	0·4	97·1
C. phlogina					
CBFS JV3437 (AP)	0·6	2·2	1·2	0·7	95·3
CBFS JV3437 (TH)	0·6	2·2	1·2	0·7	95·3

parsimony analysis yielded 67 islands of equally parsimonious trees with the length of 417 steps (due to the `nchuck` setting, each island contains 3 trees and may in fact represent a fraction of a larger island). The consistency index (CI) of the trees was 0·695 and the retention index (RI) 0·640. The bootstrap tree showed 40 supported internodes (BS > 50%). The phylogenetic tree, based on the Bayesian inference analysis is presented here (Fig. 1) along with the posterior probabilities (PP) for the nodes. Since the parsimony bootstrap search yielded a tree topologically congruent with Fig. 1, yet less resolved (there were 52 internodes supported by the Bayesian inference), we are adopting only bootstrap values (BS) from this analysis. Two groups, recognized by the parsimony bootstrapping, but collapsed in the Bayesian inference (clade with *C. arcisproxima* and a grouping of three *C. austrocitrina* sequences), are also depicted in Fig. 1, using additional brackets. Molecular data revealed eleven, partly semi-cryptic species present in the Black Sea region, of which five (*Caloplaca arcisproxima*, *C. austrocitrina*, *C. communis*, *C. confusa*, and *C. nigromarina*) are proposed here as species new to science. Three specimens were classified as *Caloplaca* sp. because they do not fit any recognized species, but they comprise insufficient material to merit the description of new species. It seems probable that more species of *Caloplaca* remain to be discovered in the Black Sea region.

Above species level, the molecular analysis revealed four large, internally diverse groups in the '*Caloplaca citrina* clade'. The first and most basal comprises *C. citrina*, *C. havaasii*, *C. ora* p.p., *C. maritima* and *C. communis* (PP = 0·99 and BS = 97). The second group, formed by *C. calcitrapa*, *C. nigromarina*, *C. marina*, *C. microthallina* and *C. confusa* has a rather low support (PP = 0·91, BS = 37). The third group includes *C. flavocitrina* and *C. geleverjae* (PP = 1·00, BS = 89), while the fourth includes *C. dichroa*, *C. austrocitrina*, *C. limonia*, *C. arcis* and *C. arcisproxima* (PP = 0·93, BS = 30). The backbone of the tree is, however, not strongly supported, which is not surprising when using only the ITS sequences.

Morphology

Thallus morphology of the *Caloplaca citrina* clade is very variable. It contains species with soredia (47% of the species examined), blastidia (12%), a granular thallus surface (12%), and a thallus without vegetative diaspores (29%). The size of soredia, blastidia or granules is a useful key character in some species (Fig. 4). The thallus is always autotrophic and lichenicolous species are probably absent from this group. It varies from yellow to orange (only exceptionally grey, in *Caloplaca geleverjae*) and may be continuous or formed of discrete granules, areoles or squamules, up to 550 μm thick and up to 2·7 mm diam. The true cortex is usually inconspicuous, formed of 1–2 layers of cells. The alveolate cortex (for details see Materials and Methods) is more distinctly developed, up to *c.* 50 μm thick, paraplectenchymatous and formed of thin-walled cells, (3·0–) 5·4 ± 1·1 (–10·0) μm diam. (n = 479). An epinecral layer is usually present, but thin, up to *c.* 20 μm thick. The algal layer fills most of the thallus interior and is made up of algal cells (5·0–) 11·4 ± 3·3 (–32·0) μm diam. (n = 537) as well as ± isodiametric fungal cells, (3·0–) 5·2 ± 1·2 (–9·0) μm diam. (n = 537). The medulla is mostly inconspicuous, formed of loose hyphal strands. In sorediate species, the development of the soralia differs markedly between species and provides important key characters. Three different types are described here (Fig. 2); the '*confusa*-type', where blastidia are produced first at the margins of the areoles and ± labriform soralia develop after the blastidia have eroded or have been shed; the '*flavocitrina*-type', where soredia are produced directly in well-delimited labriform or rarely laminal soralia; and the '*limonia*-type', where blastidia first build up on the thallus surface, and true soralia are produced from cracked blastidia or after the blastidia have eroded. These three types of development are hardly recognizable when the thallus is too young or over mature and forming entire sorediate crusts. Soredia may be single, *c.* 20–60 μm diam., or grouped in consoredia.


C. holocarpa AF353945
C. citrina DQ17322
C. citrina DQ173223
C. citrina DQ173226
C. citrina EU563387
C. citrina DQ173222
C. citrina DQ173224
C. havaasii DQ647649
C. ora EU563412
C. maritima EU563462
C. maritima AF353948
C. maritima EU563451
C. communis EU563409
C. communis EU563410
C. communis EU563446
C. communis EU563447
C. communis EU563448
C. communis EU563399
C. communis EU563397
C. communis EU563411
C. communis EU563437
C. communis EU563396
C. communis EU563429
C. calcitrapa EU563401
C. calcitrapa EU563431
C. calcitrapa DQ173227
C. calcitrapa EU563444
C. sp. EU563433
C. nigromarina EU563436
C. nigromarina EU563418
C. nigromarina EU563459
C. nigromarina EU563398
C. nigromarina EU563393
C. nigromarina EU563394
C. nigromarina EU563430
C. marina EU563461
C. marina EU563470
C. marina AF353947
C. marina AF353946
C. microthallina EU563463
C. microthallina EU563464
C. microthallina EU563469
C. microthallina EU563465
C. confusa EU563405
C. confusa EU563468
C. confusa EU563455
C. confusa EU563449
C. confusa EU563457
C. sp. EU563389
C. geleverjae EU563423
C. flavocitrina DQ173219
C. flavocitrina EU563471
C. flavocitrina EU563388
C. flavocitrina DQ173216
C. flavocitrina EU563434
C. flavocitrina EU563456
C. flavocitrina DQ173217
C. flavocitrina EU563390
C. flavocitrina DQ173218
C. flavocitrina EU563435
C. flavocitrina EU563442
C. flavocitrina EU563439
C. flavocitrina DQ173220
C. flavocitrina EU563440
C. flavocitrina DQ173221
C. flavocitrina EU563392
C. flavocitrina EU563466
C. dichroa EU563415
C. dichroa DQ173229
C. dichroa EU563458
C. dichroa DQ173232
C. dichroa DQ173230
C. dichroa EU563421
C. dichroa DQ173231
C. dichroa EU563428
C. dichroa DQ173228
C. austrocitrina EU563406
C. austrocitrina EU563416
C. austrocitrina EU563417
C. austrocitrina EU563419
C. austrocitrina EU563420
C. austrocitrina EU563441
C. austrocitrina EU563426
C. austrocitrina EU563427
C. austrocitrina EU563450
C. sp. EU563414
C. limonia EU563402
C. limonia EU563445
C. limonia EU563391
C. limonia EU563407
C. limonia EU563403
C. limonia EU563422
C. limonia EU563400
C. limonia EU563467
C. limonia EU563408
C. arcisproxima EU563413
C. arcisproxima EU563425
C. arcis EU563395
C. arcis EU563424
C. arcis EU563438
C. arcis EU563454
C. arcis DQ173215
C. arcis EU563452
C. arcis EU563453
C. arcis DQ173214
C. arcis DQ173213
0·1

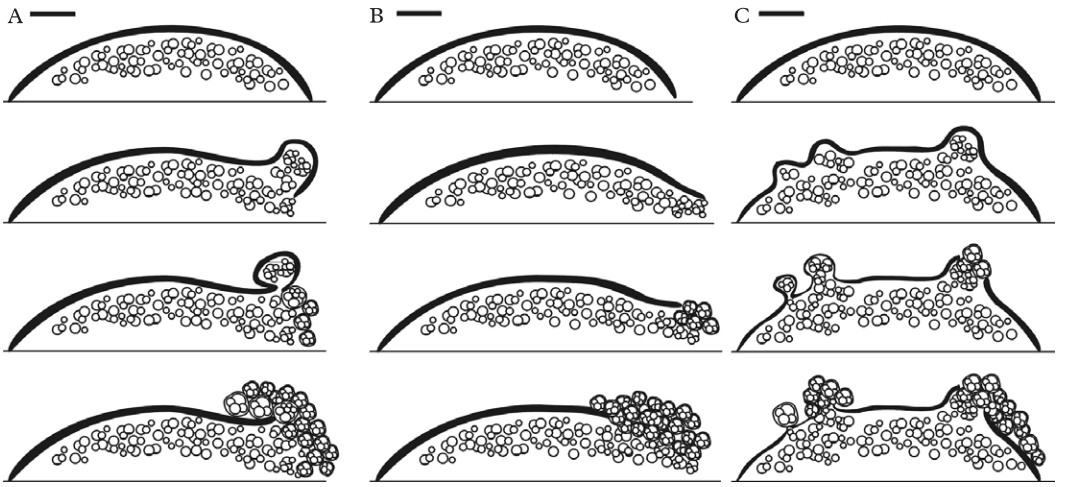


FIG. 2. Development of soralia in the *Caloplaca citrina* group. A, *confusa*-type; B, *flavocitrina*-type; C, *limonia*-type. Note that initial and late stages are almost identical in all types. Scales: A–C = 100 μm.

The apothecia are small, up to 1·6 mm diam., and sessile. Discs (slightly concave–) flat to slightly (or strongly) convex, ± uniformly orange. The apothecial margins *c.* 40–210 μm thick, ± persistent and paler than the discs, zeorine, formed of a ± prosoplectenchymatous true exciple and a thalline exciple, which may be indistinct and hidden below the true exciple in young apothecia, but raised and distinct in older ones. The hypothecium (including subhymenium) is (30–) 102 ± 31 (–230) μm thick (n = 103), formed of dense, intricate, translucent hyphae. The hymenium is *c.* 60–90 μm thick and the asci are of *Teloschistes*-type, cylindrical, (34–) 51 ± 6 (–72) × (7–) 11·5 ± 2 (–18) μm (n = 99). The ascospores are *c.* 9–17 × 4–8 μm large and belong to one of two types: the common, thin-walled '*citrina*-type' or the rare, thick-walled 'sand-clock' type (Fig. 3). The ascospore septa are *c.* 3–7 μm wide. The paraphyses are simple, branched or anastomosed, *c.* 1–2·5 μm thick, with widened tips, up to 7 μm.

The pycnidia are inconspicuous, hardly recognizable as dots with a different tinge of yellow or orange, *c.* 80–130 μm diam. The conidiophores are variable in height, branched and anastomosed in parts (Fig. 3). The conidiogenous cells are variable in shape, but mostly obtuse triangular, *c.* 4–6 μm diam. The conidia are acro- or pleurogenous, ellipsoid to bacilliform, *c.* 2–4 × 1–1·5 μm.

Chemistry

All the species treated here contain anthraquinones of the chemosyndrome A (*sensu* Søchting 1997) with parietin as a dominant compound, and small amounts of emodin, fallacinal, parietinic acid and teloschistin. This chemosyndrome is the most common within *Teloschistaceae*. No significant differences were observed among the species treated (Table 2); some minor differences are of a quantitative nature only, such as greater amounts of fallacinal in *Caloplaca arcis*, *C. austrocitrina*, *C. flavocitrina* and *C.*

FIG. 1. Bayesian consensus phylogeny of the *Caloplaca citrina* group inferred from 105 nuclear ITS sequences. Node support values (in black) are Bayesian posterior probabilities and numbers in grey represent bootstrap values obtained after 1000-times resampled parsimony heuristics (bootstrap values under 50% are not shown). Groupings recovered by parsimony heuristics yet not by the Bayesian inference are depicted by lines to the right of the tree.

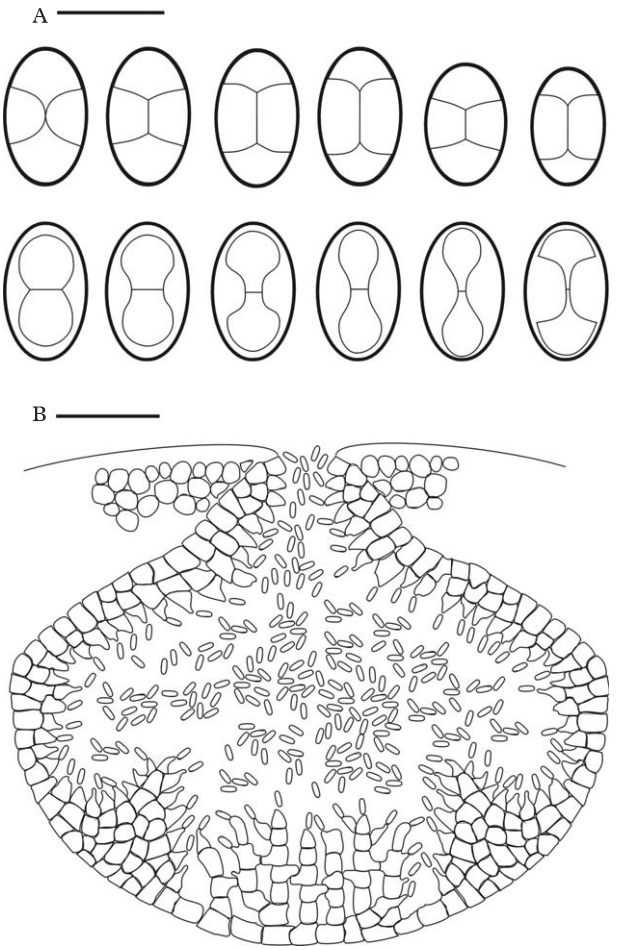


FIG. 3. *Caloplaca citrina* group. A, *C. calcitrapa* ascospores, *citrina* type spores (top row) (CBFS JV5486), sand glass type spores (bottom row) (CBFS JV6112); B, *C. communis*, vertical section of a pycnidium (CBFS JV3369). Scales: A = 10 μm; B = 20 μm.

nigromarina, than in the rest of species treated. The thallus cortex and the apothecia are K+ violet, C−, P−, UV± orange. In sections, the hymenium and the subhymenium are I+ blue, but the true exciple is I−. Exceptionally, in *Caloplaca geleverjae*, anthraquinones are absent from the K− thallus.

Phenotypic variability and the taxonomic value of the characters

In most of the characters studied, pronounced phenotypic variability was observed. Some extreme examples of variability in width of the areoles, size of vegetative diaspores, width of the exciple, the hymenium thickness, width of paraphysis tips and ascospore characters are shown for particular species in Fig. 4. In these characters, there are no, or only small, overlaps in dimensions between different specimens of the same species making it difficult to find diagnostic morphological characters.

A comparison of the species treated using vegetative diaspore, thallus thickness and ascospore characters is shown in Fig. 5. Some species may be grouped, such as *Caloplaca communis*, *C. geleverjae* and *C. limonia*

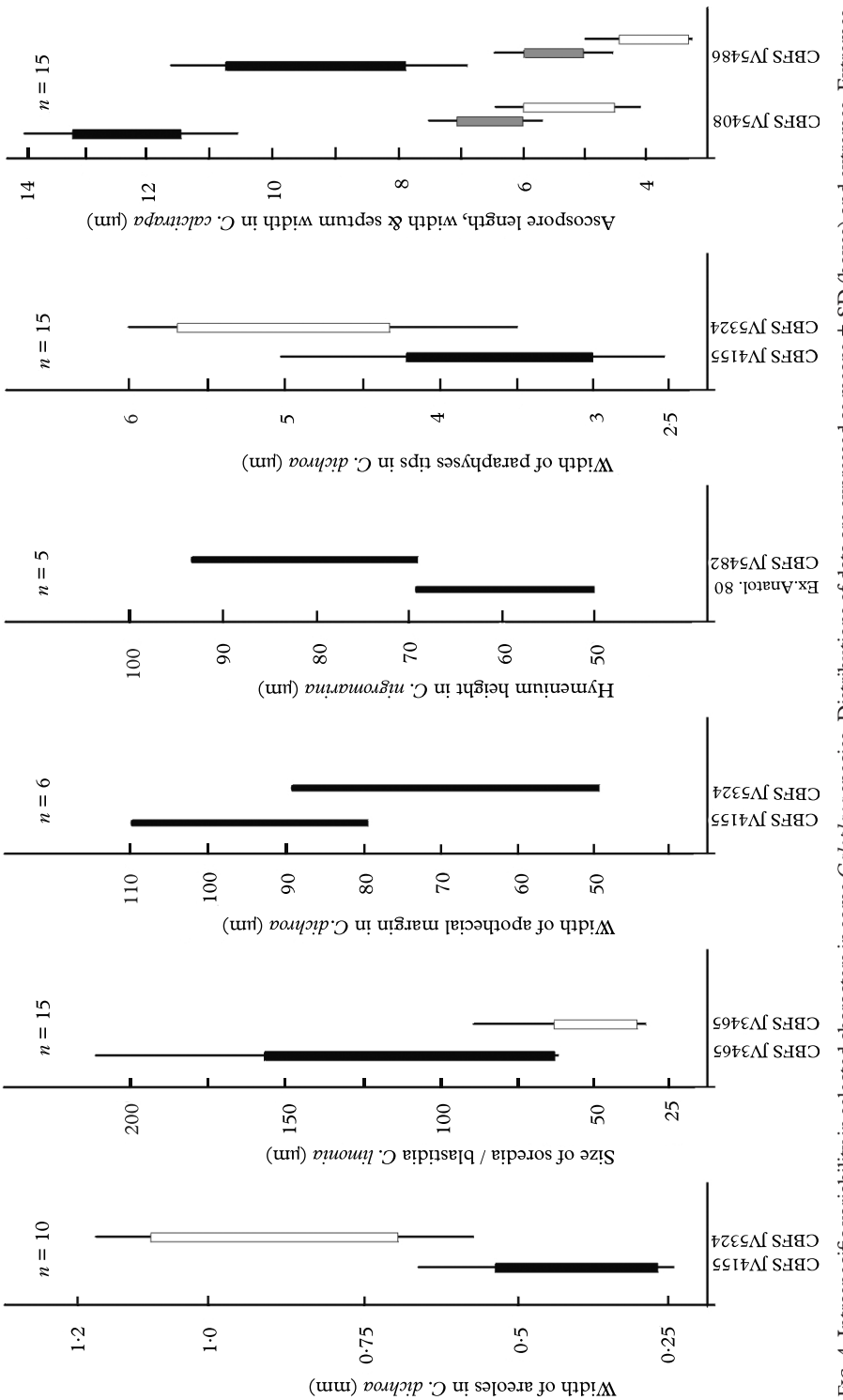


FIG. 4. Intraspecific variability in selected characters in some *Caloplaca* species. Distributions of data are expressed as means ± SD (boxes) and extremes. Extremes depicted when $n \geq 10$. Sample accession numbers and numbers of measurements are given at the bottom and top, respectively.

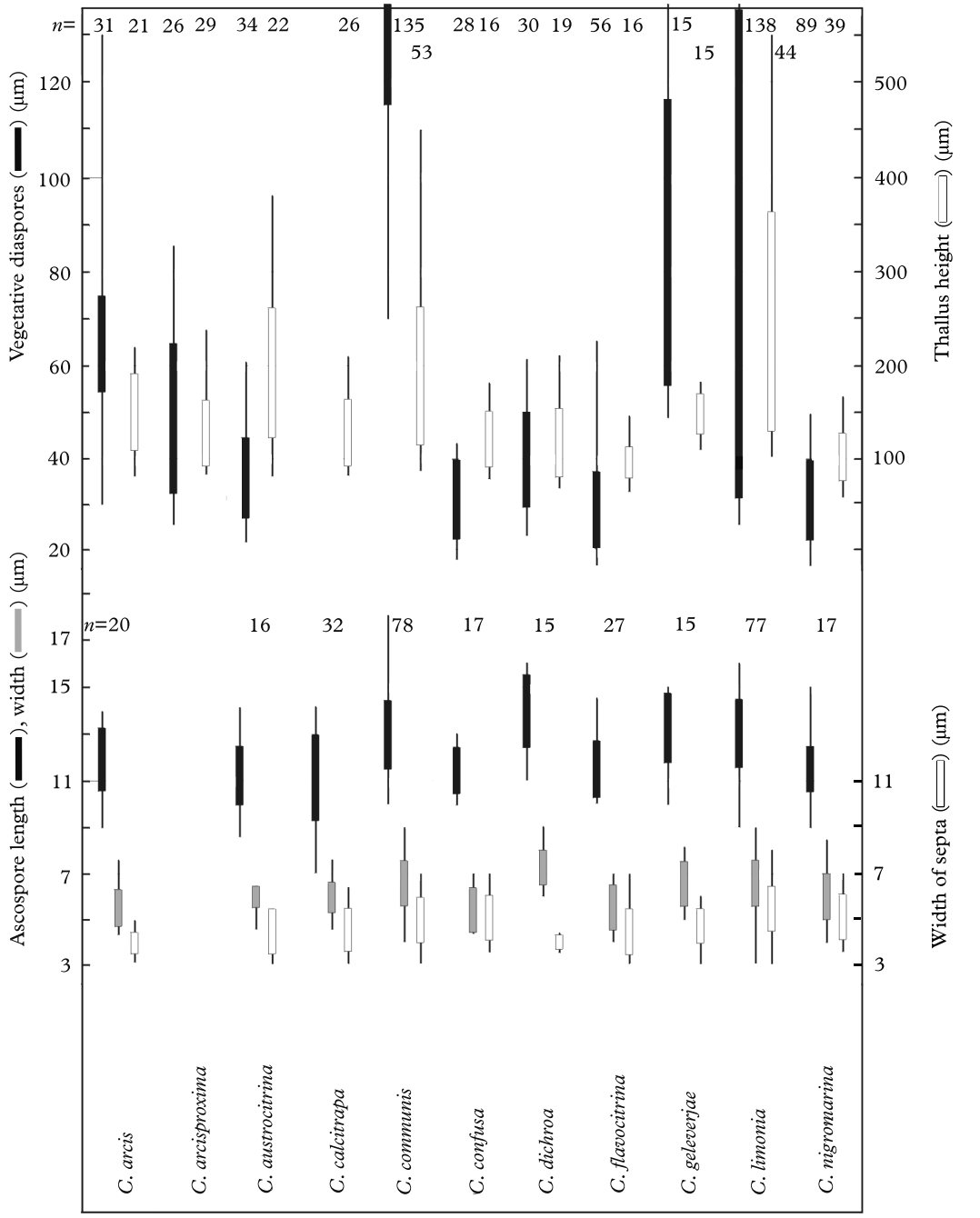


FIG. 5. Variability in some characters among the *Caloplaca* species treated. Distributions of data are expressed as mean ± SD (boxes) and extremes.

TABLE 3. *List of species with the* Caloplaca citrina *morphology occurring on seashore cliffs in the Northern Hemisphere with data on their distributions and references. Species marked by ** are treated here in detail; those marked by * are treated briefly under notes on other species*

Species	†	Distribution / ecology	References
C. arcis (Poelt & Vězda) Arup **	Cc	Europe, Mediterranean, the Black Sea region	Arup 2006*a*; this paper
C. arcisproxima Vondrák, Arup & Søchting sp. nov. **	Cc	Black Sea coast, eastern Mediterranean	This paper
C. austrocitrina Vondrák, Arup & Søchting sp. nov. **	Cc	Central, eastern and southern Europe; mostly on concrete	This paper
C. bolacina (Tuck.) Herre		Western coast of North America	Arup 1993*b*, 1995*b*
C. britannica R. Sant. *		British Isles; restricted to maritime rocks	Laundon 1992*b*
C. calcitrapa Nav.-Ros., Gaya & Cl. Roux) **	Cc	Black Sea coast, Mediterranean; on calcareous sea-shore rocks, if inland?	Navarro-Rosinés *et al.* 2000; this paper
C. citrina (Hoffm.) Th. Fr. *	Cc	Northern and central Europe, elsewhere not confirmed	Arup 2006*a*
C. communis Vondrák, Arup & Søchting sp. nov. **	Cc	Black Sea coast, eastern Mediterranean	This paper
C. confusa Vondrák, Arup & Søchting sp. nov. **	Cc	Black Sea coast, Mediterranean, Azores	This paper
C. coronata (Kremp. ex Körb.) J. Steiner		Europe; mostly on inland calcareous rocks	e.g. Foucard 2001
C. dichroa Arup **	Cc	Europe; mostly on inland calcareous rocks	Arup 2006*a*; this paper
C. flavocitrina (Nyl.) H. Olivier **	Cc	Europe, North America (confirmed from Hawaii), Asia?; epiphytic or epilithic, mostly inland species	Arup 2006*a*; Vondrák *et al.* 2007; this paper
C. flavogranulosa Arup		Western coast of North America	Arup 1993*a*, 1995*b*
C. geleverjae Khodosovtsev & S. Kondr. **	Cc	Crimean Peninsula; coastal cliffs	Khodosovtsev *et al.* 2003; this paper
C. havaasii H. Magn.	Cc	Norway; known only from type locality, inland; occurrence on maritime cliffs not confirmed	Arup 2006*c*
C. inconnexa (Nyl.) Zahlbr.		Mediterranean, Europe; often lichenicolous, e.g. on *Acarospora cervina*	Vondrák *et al.* 2007
C. inconnexa var. *nesodes* Poelt & Nimis (?= *C. necator* Poelt & Clauzade)		Black Sea coast, Mediterranean; lichenicolous on *Aspicilia*	Nimis & Poelt 1987
C. inconspecta Arup	?	Western coast of North America	Arup 1995*a*, *b*
C. limonia Nimis & Poelt **	Cc	Mediterranean, Black Sea region, East and Central Europe	Nimis *et al.* 1994; this paper
C. littorea Tav.	?	Atlantic coast of Europe	Laundon 1992a; Tavares 1956
C. luteominia (Tuck.) Zahlbr.		Western coast of North America	Arup 1993b, 1995*b*
C. ludificans Arup	?	Western coast of North America	Arup 1995*a*,*b*
C. marina (Wedd.) Zahlbr. (syn.: *C. marina* subsp. *americana* Arup) *	Cc	Western coast of North America and Atlantic coast of Europe	Arup 1992*a*, 1995*b*, 1997; Nordin 1972
C. maritima (B. de Lesd.) B. de Lesd. *	Cc	Atlantic coast of Europe, West Mediterranean	Arup 1997
C. microthallina (Wedd.) Zahlbr. *	Cc	Scandinavian coast, Atlantic coast of Europe and North America	Arup 1994, 1997*b*; Laundon 1992*a*; Nordin 1972
C. nigromarina Vondrák, Arup & Søchting sp. nov. **	Cc	Black Sea coast	This paper

TABLE 3. *Continued*

Species	†	Distribution / ecology	References
C. ora Poelt & Nimis*	Cc	Mediterranean	Nimis & Poelt 1987
C. phlogina (Ach.) Flag.*		Europe; mostly on bark or shrub twigs but also on concrete close to sea shore	Arup 2006*a*; Vondrák *et al.* 2007
C. rosei Hasse		Western coast of North America	Arup 1992*a*, 1995*b*
C. ruderum (Malbr.) J. R. Laundon	?	Great Britain, Continental Europe?; on mortar and soft limestone in walls, if on coastal cliffs?	Laundon 1976
C. sorediella Arup		Great Britain, coastal rocks	Arup 2006*b*
C. soropelta (Hansen, Poelt & Søchting) Søchting		Greenland and Svalbard	Hansen *et al.* 1987; Søchting 1992
C. thamnoblasta Nimis & Poelt		Mediterranean; on calcareous sea-shore rocks	Vězda 1993

† column: Cc indicates species belonging to the *Caloplaca citrina* clade; ? position of species uncertain.

that have larger vegetative diaspores, or *C. austrocitrina*, *C. communis* and *C. limonia* that have larger areoles, whereas *C. dichroa* has somewhat wider ascospores and *C. arcis* and *C. dichroa* have thinner spore septa. However, the characters are much less useful in a single sample, which may possess only a part of a range of variability. For example, specimens of *C. limonia* from shaded places have significantly smaller soredia than samples from sun-exposed rock faces, which produce blastidia rather than soredia.

Useful key characters are mainly vegetative, such as thallus colour, presence of different vegetative diaspores of different sizes, development of soredia and thickness of the thallus and size of areoles. Apothecial characters (e.g. ascospore size and width of spore septa) where there is often strong phenotypic variability and small differences between species are less useful. Moreover, the sorediate species are rather sparingly fertile and *C. arcisproxima* is not known fertile.

Short diagnostic description of Caloplaca citrina *group.*

Thallus yellow to orange (except for *Caloplaca geleverjae*), continuous or made up of dispersed granules, areoles or squamules. Vegetative diaspores, such as soredia and blastidia are often present. Apothecia small with orange discs and zeorine margins. True exciple of elongated cells. Ascospores thin-walled (except for some specimens in *C. calcitrapa* and *C. dichroa*), with thick septa.

Unfortunately, these morphological characters are shared with other, phylogenetically unrelated species, for example, members of the *Caloplaca dolomiticola* group. The position of each species must therefore be confirmed by molecular data. Some superficially similar species of the *Caloplaca lactea* group (e.g. *C. crenulatella* and *C. interfulgens*) and of the *C. squamosa* group (e.g. *C. subsoluta*) do not fit the '*Caloplaca citrina* morphology'. The former has large, narrow-ellipsoid ascospores with thin septa (Navarro-Rosinés & Hladun 1996) and the latter has a paraplectenchymatous true exciple (Arup 1992*b*; Wetmore 2003).

Species with the '*Caloplaca citrina* morphology' occurring on seashore cliffs are listed in Table 3. It is noted there that not all of the species belong to the *Caloplaca citrina* clade.

Key to the saxicolous *Caloplaca* species occurring on coastal cliffs in the Black Sea region

1 Thallus pale grey, rarely slightly yellow, formed of areoles ± entirely covered by blastidia. . . . . **C. geleverjae**
Thallus yellow to orange, in shaded sites pale-yellow to yellow-grey 2

2(1) Soredia absent, but blastidia may be present 3
Soredia present, thallus sometimes blastidiate only, but in well-developed populations, soredia always present where blastidia have eroded (*limonia*-type of soralia) 5

3(2) Vegetative diaspores absent, but large thallus granules may be present 4
Blastidia present on surface and at margins of inner areoles, (30–) 75 ± 21 (–130) μm, thallus usually with short-lobed margins . . . . . **C. arcis**

4(3) Thallus variable, consisting of convex areoles, (90–) 190 ± 75 (–450) μm thick, with granular surface, or thallus formed by dispersed granules; granules (70–) 180 ± 66 (–380) μm, apothecia usually abundant, large, (0·2–) 0·6 ± 0·2 (–1·3) mm diam., often with crenulate margin; common on hard siliceous coastal rocks . . . . . **C. communis**
Thallus of flat to convex areoles, only (80–) 129 ± 36 (–210) μm thick; surface smooth, not granular, on coastal limestone or lime-rich schistose rocks . . . . . **C. calcitrapa**

5(2) Thallus thin, up to 200 μm thick, areolate, never squamulose, composed of a greyish-yellow to yellow sorediate crust only, soredia small (20–) 42 ± 14 (–63) μm; epiphytic or on loess and concrete; not found on rock . . . . . **C. phlogina**
Thallus mainly thicker, up to 550 μm thick, soredia on average larger, 23–320 μm, of *confusa*, *flavocitrina* or *limonia*-type (Fig. 2); known from coastal cliffs 6

6(5) Soralia ± delimited, developing mainly from margins of areoles (*confusa* or *flavocitrina*-type of soralia), but old thalli may be entirely sorediate 8
Soralia not delimited, of *limonia*-type; thallus often entirely sorediate/blastidiate 7

7(6) Thallus (100–) 248 ± 111 (–550) μm thick, dull to bright yellow, sometimes with minute marginal lobes, sorediate; soredia coarse, (26–) 85 ± 54 (–320) μm, old thalli may form a thick, entirely sorediate crust . . . . . **C. limonia**
Thallus (70–) 118 ± 36 (–210) μm thick, yellow or orange, without marginal lobes, areoles ± entirely sorediate/blastidiate, vegetative diaspores smaller, (23–) 40 ± 11 (–61) μm diam., usually both, orange and yellow thallus morphs are present in the localities . . . . . **C. dichroa**

8(6) Thallus of ± umbilicate squamules, with margins divided into minute lobes . . . . . **C. arcisproxima**
Thallus areolate or squamulose, but not with margins divided into minute lobes 9

9(8) Thallus areolate (rarely squamulose), (80–) 192 ± 70 (–380) μm thick, areoles (squamules) large, (0·25–) 0·74 ± 0·32 (–1·7) mm wide, old thalli usually entirely covered by soredia; mainly on concrete . . . . . **C. austrocitrina**
Areoles/squamules smaller, up to 180 μm thick and up to 1·4 mm wide; thallus usually not forming entire sorediate crust 10
(a difficult species, lacking sufficient diagnostic morphological characters)

10(9) Thallus mostly yellow, soralia of *flavocitrina* type predominate; if on coast, then usually on calcareous substrata (concrete, calcareous sandstones, etc.) . . . . . **C. flavocitrina**
Thallus mostly yellow-orange (in shaded sites yellow); on siliceous coastal cliffs 11

11(10) *Confusa*, *flavocitrina* and *limonia* types of soralia present . . . . . **C. confusa**
Only *confusa* and *flavocitrina* types of soralia present . . . . . **C. nigromarina**

Taxonomy

Caloplaca arcis (Poelt & Vězda) Arup

Lichenologist **38:** 8 (2006).—*Caloplaca citrina* var. *arcis* Poelt & Vězda in Vězda, *Lichenes Selecti Exsiccati, fasc.* 99 (1990); type: Austria, Styria, distr. Feldbach, Riegersburg, alt. 400 m, on andesite rock, 1990, *G. Kantvilas, H. Mayrhofer & A. Vězda* (A. Vězda: *Lich. Sel. Exsicc.* 2470, BM!, PRM!—isotypes).

(Fig. 6A & B)

Thallus yellow, areolate or formed of tightly aggregated squamules; marginal areoles have a ± lobate character. Areoles/squamules (80–) 150 ± 39 (–220) μm thick (n = 21) and (0·3–) 1·11 ± 0·7 (–3·0) mm wide (n = 47). Thallus surface smooth or covered by granules and blastidia; in old thalli, vegetative diaspores may cover most of the thallus surface. Granules/blastidia (30–) 75 ± 21 (–130) μm diam. (n = 31). *Cortex* indistinct, alveolate cortex (7–) 18 ± 8 (–32) μm high (n = 18).

Apothecia present in 37% of investigated specimens, (0·41–) 0·6 ± 0·13 (–0·88) mm diam. (n = 19). Discs slightly concave to flat. *Exciple* (70–) 105 ± 21 (–140) μm thick (n = 15), zeorine, sometimes crenulate. The true exciple/thalline exciple ratio very variable; thalline exciple enlarged with age. *Hymenium* 70–100 μm thick (n = 12). *Paraphyses* tips widened to (3·0–) 4·4 ± 0·6 (–5·5) μm (n = 27). *Ascospores* (9·0–) 12·0 ± 1·25 (–14·0) × (4·5–) 5·5 ± 0·9 (–7·5) μm (n = 20); length/breadth ratio *c.* 2·2; ascospore septa (3·0–) 4·0 ± 0·5 (–5·0) μm thick (n = 20), *c.* 0·33 of ascospore length.

Conidia (1·5–) 2·4 ± 0·5 (–3·0) × (1·0–) 1·25 ± 0·25 (–1·5) μm (n = 26).

Remarks. This species is characterized mainly by its blastidiate thallus with short-lobed margins. In some cases, it is hardly distinguishable from *Caloplaca limonia*, but in well-developed populations, *C. arcis* has distinct marginal lobes, and blastidia (soredia are absent) are restricted to central parts of the thallus; whereas *C. limonia* often has an entirely sorediate/blastidiate thallus surface.

Phylogeny. According to the DNA analyses, *Caloplaca arcis* forms a well-supported monophyletic group (PP 1·00, BS = 98) with two sequences of *C. arcisproxima* in a sister position and *C. limonia* as the second closest taxon.

Ecology and distribution. Caloplaca arcis occurs mainly on inland sun-exposed, hard siliceous, but usually base-rich rock faces. Although it is also known from pure limestone (Arup 2006*a*), it was not found on calcareous substrata in the Black Sea region. When it occurs on coastal rocks, it usually avoids the supralittoral zone (Kiten, Bulgaria, extremely sheltered shore: from 1 m upwards; Sinop, Turkey, extremely exposed shore: from 130 m upwards). Accompanying species: *Caloplaca* aff. *furax*, *C. teicholyta*, *C. thracopontica*, *Candelariella plumbea*, *Catillaria chalybeia*, *Diplotomma alboatrum* s. lat., *Lecanora albescens*, *L. campestris*, *Phaeophyscia orbicularis*, *Verrucaria macrostoma* f. *furfuracea*, and *Xanthoria* cf. *calcicola*. The species is widely distributed in Europe. Here, it is newly recorded from Bulgaria, Italy, the Netherlands, Slovakia, Turkey and the Canary Islands.

Specimens examined. **Bulgaria:** *Black Sea coast:* Burgas, Tsarevo, Rezovo, 2005, *J. Vondrák* (CBFS JV3036); Burgas, Kiten, rocks near mouth of Karaagach river S of town, 2007, *J. Vondrák* (CBFS JV6093).—**Italy:** *Sardinia*: Arburese, on volcanic rock alt. 320–380 m, 1986, *W. Brunnbauer* (GZU, sub *C. citrina*).—

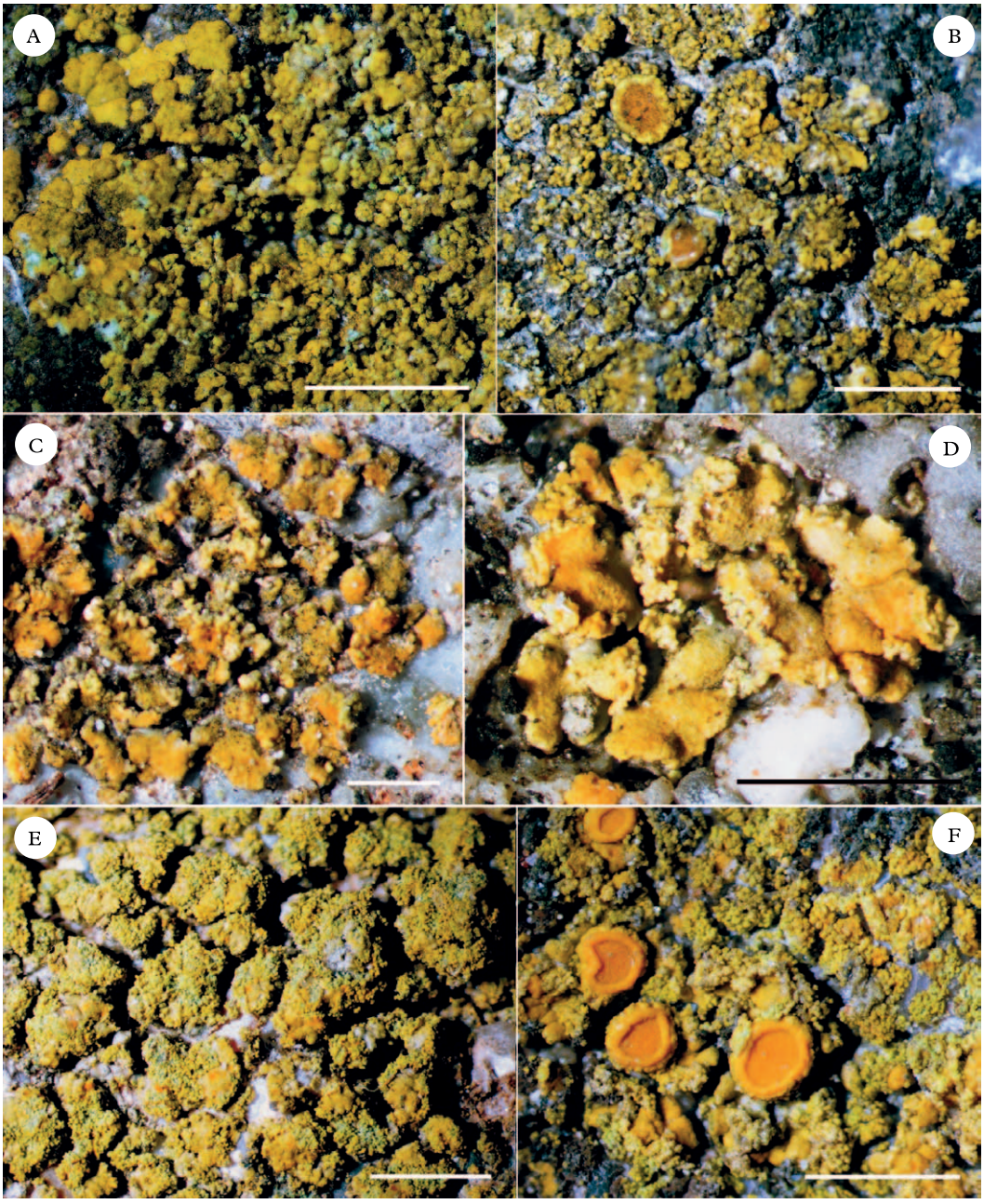


FIG. 6. Morphology of *Caloplaca* species. A & B, *Caloplaca arcis*; C & D, *C. arcisproxima*; E & F, *C. austrocitrina*. Scales: A–F = 1 mm.

The Netherlands: Liemers, 2003, *A. Aptroot* 59582 (ABL); Zwartemeerdijk, 2004, *A. Aptroot* 59871 (ABL).—**Slovakia:** *Muránská planina Mt:*. in valley Hrdzavá, a1t. 1220–1270 m, 1999, *A. Guttová, J. Halda & Z. Palice* (SAV, sub *C. citrina*).—**Spain:** *Canary Islands*: Tenerife, Aguamansa, 1986, *W. Brunnbauer* (W, sub *Caloplaca* sp.).—**Turkey:** *Black Sea coast*: Sinop, alt. *c.* 100 m, 2007, *J. Vondrák* (CBFS JV5426, 6106).

Caloplaca arcisproxima Vondrák, Říha, Arup & Søchting sp. nov.

Thallus squamulis umbilicatis (0·44–) 0·78 ± 0·21 (–1·18) mm latis contextus, margo squamularum in lobulos minutos divisus. Soralia typo *C. confusae* vel *flavocitrinae*.

Typus: Ukraine, Crimean Peninsula, Alushta, coastal rocks SW of Ribachye, 44°45′35.36″N, 34°35′10.30″E, on supralittoral diabasic rock, 27 May 2007, *J. Vondrák* (CBFS JV5473—holotypus; CBFS JV6038, hb. C & LD—isotypi). ITS sequence of the holotypus: EU563425.

(Fig. 6C & D)

Thallus yellow to yellow-orange, of solitary or rarely aggregated, ± umbilicate squamules. Squamules (80–) 129 ± 36 (–240) μm thick (n = 29) and (0·44–) 0·78 ± 0·21 (–1·18) mm wide (n = 22). Squamules flat, smooth, with margins divided into minute lobes. Marginal soralia of *confusa* or *flavocitrina* type. Soredia/blastidia (25–) 48 ± 16 (–86) μm diam. (n = 26). *Cortex* indistinct, alveolate cortex (8–) 24 ± 9 (–46) μm thick (n = 36).

Apothecia absent in specimens investigated.

Conidia (2·5–) 3·0 ± 0·3 (–4·0) × (0·5–) 1·0 ± 0·25 (–1·5) μm (n = 15).

Etymology. *Arcisproxima* means close to *arcis*. The new species is phylogenetically close to *Caloplaca arcis* and the species also share some morphological characters (e.g., distinct squamules).

Remarks. The species is characterized mainly by its umbilicate squamules, with margins divided into minute lobes and by the presence of soralia of *confusa* or *flavocitrina* types. The species may be confused with *Caloplaca confusa*, *C. flavocitrina* or *C. nigromarina*, but it differs in its ± umbilicate squamules, with somewhat raised margins. It somewhat resembles *C. arcis* in its squamules, which are often divided into minute lobes, but *C. arcisproxima* differs in the presence of *confusa* or *flavocitrina* types of soralia.

Phylogeny. The monophyly of the two sequences obtained from *Caloplaca arcisproxima* was not confirmed by the parsimony analysis (BS = 70%) or the Bayesian inference. However, this may be due to poor lineage sorting in a young species or to the fact that only two specimens have been analysed. A close affinity to *C. arcis* is shown (PP = 1·00), but the two species clearly differ from each other in their morphology.

Ecology and distribution. Based on the known localities, the species prefers base-rich, hard siliceous rocks (e.g. diabasic), but was found also on ±soft, lime-rich claystone. It is known only from maritime sites, usually from the supralittoral zone. Accompanying species: *Caloplaca* cf. *aegea*, *C. biatorina* s. lat., *Caloplaca* aff. *furax*, *C. teicholyta*, *Candelariella plumbea*, *C. vitellina*, *Catillaria chalybeia*, *Diplotomma alboatrum* s.lat., *Lecanora albescens*, *L. dispersa* s. lat., *Phaeophyscia orbicularis*, *Verrucaria macrostoma* f. *furfuracea*, and *Xanthoria* cf. *calcicola*. The species is so far known from the Crimean Peninsula in the Black Sea region and Crete in the eastern Mediterranean.

Specimens examined: **Ukraine:** *Crimean Peninsula*:. Cape Meganom, 2002, *A. Khodosovtsev* (KHER 3030, sub *C. citrina*).—**Greece:** *Crete*: Agios Pavlos, alt. *c.* 215–240 m, 1997, *H. Mayrhofer* (GZU); Ano Viannos, Sidonia, alt 10–50 m, 2005, *J. Vondrák* (CBFS JV4125); Mires, Kali Limenes, siliceous rock, alt. *c.* 100 m, 2005, *J. Vondrák* (CBFS JV3877).

Caloplaca austrocitrina Vondrák, Říha, Arup & Søchting sp. nov.

Caloplacae citrinae similis, differt thallo areolato (raro squamuloso) (80–) 192 ± 70 (–380) μm crasso, areolisque (squamulis) majoribus (0·25–) 0·74 ± 0·32 (–1·7) mm latis. Soralia typo *C. flavocitrinae*. Praecipue in operi concreto habitat.

Typus: Ukraine, Crimean Peninsula,. Alushta (Алушта), slopes above sea *c.* 1 km SW of Semidvorje (Семидворье), alt. *c.* 100 m, 44°42′48.10″N, 034°27′12.10″E, on vertical side of concrete wall, 13 June 2006, *J. Vondrák* (CBFS JV5236—holotypus; CBFS JV5285, LD—isotypi). ITS sequence of the holotypus: EU563419

(Fig. 6E & F)

Thallus yellow, rarely orange (e.g. the specimen from Crete), areolate or formed of tightly aggregated squamules. Areoles/

squamules (80–) 192 ± 70 (–380) µm thick (n = 22) and (0·25–) 0·74 ± 0·32 (–1·7) mm wide (n = 51). Squamules flat, smooth, with marginal soralia of *flavocitrina* type; in old thalli, soralia may cover the whole thallus surface. Soredia (22–) 36 ± 10 (–61) µm diam. (n = 34), sometimes gathered to consoredia. *Cortex* or alveolate cortex developed, (6–) 19 ± 8 (–40) µm thick (n = 30).

Apothecia present in 50% of the specimens investigated, (0·32–) 0·46 ± 0·1 (–0·65) mm diam. (n = 16). Disc in mature apothecia flat to convex. *Exciple* (50–) 86 ± 20 (–130) µm thick (n = 16), zeorine; in young apothecia, the thalline exciple is hidden below the true margin while in old apothecia, the thalline exciple is well-developed and persisting. *Hymenium* 60–80 µm thick (n = 5). *Paraphyses* tips widened to (3·0–) 4·4 ± 0·9 (–6·0) µm (n = 15). *Ascospores* (8·5–) 11·25 ± 1·5 (–140) × (4·5–) 6·0 ± 0·5 (–6·5) µm (n = 16); length/breadth ratio *c.* 1·88. Ascospore septa (3·0–) 4·5 ± 1·0 (–5·5) µm thick (n = 16), *c.* 0·4 of ascospore length.

Conidia (2·0–) 2·8 ± 0·5 (–4·0) × (1·0–) 1·2 ± 0·2 (–1·5) µm (n = 15).

Etymology. The name reflects the distribution of the species in Europe.

Remarks. This species is distinguished by its thick, areolate thallus (rarely squamulose), its large areoles (squamules), and its soralia of the *flavocitrina* type. Old thalli are usually entirely covered by soredia. *Caloplaca flavocitrina*, occurring on the same kind of substratum (predominantly concrete), differs in its thinner and smaller squamules.

Phylogeny. Although morphologically distinguishable, the specimens of *C. austrocitrina* do not receive any support as a monophyletic taxon, but this does not preclude possible monophyly in other genes. More work on other genes may resolve the phylogeny of *C. austrocitrina*, but the lineage sorting among other genes may also be poor. In the phylogenetic analysis *C. austrocitrina* groups with *C. limonia*, *C. arcisproxima* and *C. arcis* (PP = 0·92).

Ecology and distribution. Most of the records are from lime-rich artificial substrata, for example, concrete and mortar, but the species is also known from limestone. It occurs inland as well as in coastal areas and does not avoid substrata close to sea level, for example faces of concrete walls in harbours. Accompanying species: *Caloplaca aurantia*, *C. biatorina* s. lat., *C. crenulatella*, *Candelariella aurella*, *Lecania leprosa*, *Lecanora albescens*, *L. dispersa*, *L. muralis*, *Rinodina pityrea*, *Verrucaria macrostoma* f. *furfuracea*, and *V. muralis*. The species is probably common in south-eastern Europe and is also known from central Europe (Austria, Czech Republic and Germany) and the European part of Russia.

Selected specimens examined. **Austria:** *Styria*: Jogland, Miesenbach, alt. *c.* 1040 m, 2003, *J. Hafellner* (GZU, sub *C. citrina*).—**Bulgaria:** *Black Sea coast*: Burgas, Pomorie, 2005, *J. Vondrák* (CBFS JV4631).—**Czech Republic:** *South Bohemia*: České Budějovice, 2003, *J. Vondrák* (CBFS JV991).—**Germany:** *Bavaria*: Munich, 1978, *E. Albertshofer & H. Hertel* (W, *Lich. Alpium* 328, sub *C. citrina*).—**Greece:** *Crete*: Rethimno, ruin of fort Fortezza, 2005, *J. Vondrák* (CBFS JV4195).—**Romania:** *Dobrogea*: Romania, Tulcea, near shore of Razim Lake (Lacul Razim), 2007, *J. Vondrák* (CBFS JV6168).—**Russia:** *Black Sea coast*: Novorossiysk, coastal rocks near Dyurso, 2007, *J. Vondrák* (CBFS JV5474, dupl. in C); Sochi, coast 2 km SE of Loo, 2007, *J. Vondrák* (CBFS JV6097, 6166).—**Slovakia:** *Bukovské vrchy hills*: Nová Sedlica, 1989, *I. Pišút* (SAV, sub *C. citrina*). *Podunajská nížina lowland*: Vrakúň, 1990, *I. Pišút* (SAV, sub *C. citrina*).—**Ukraine:** *Black Sea coast*: Odessa, Czernomorskoye, 2007, *J. Vondrák* (CBFS JV5476, dupl. in LD).

Caloplaca calcitrapa Nav.-Ros., Gaya & Cl. Roux

Bull. Soc. linn. Provence **51:** 147 (2000); type: France, Eastern Pyrenees, Languedoc Roussellon, Tautavel, alt. 400–450 m, on calcareous rock (BCC 13385, holotypus). ITS sequence of an isotype: DQ173227.

(Fig. 7A & B)

Thallus yellow, rarely orange, areolate or bullate, occasionally thin with a rather endolithic character. Snail-grazed forms with flat areoles are common. Areoles (80–) 129 ± 36 (–210) µm thick (n = 26) and (0·32–) 0·52 ± 0·16 (–0·97) mm wide (n = 20). Vegetative diaspores absent. *Cortex* indistinct, alveolate (8–) 25 ± 9 (–35) µm thick

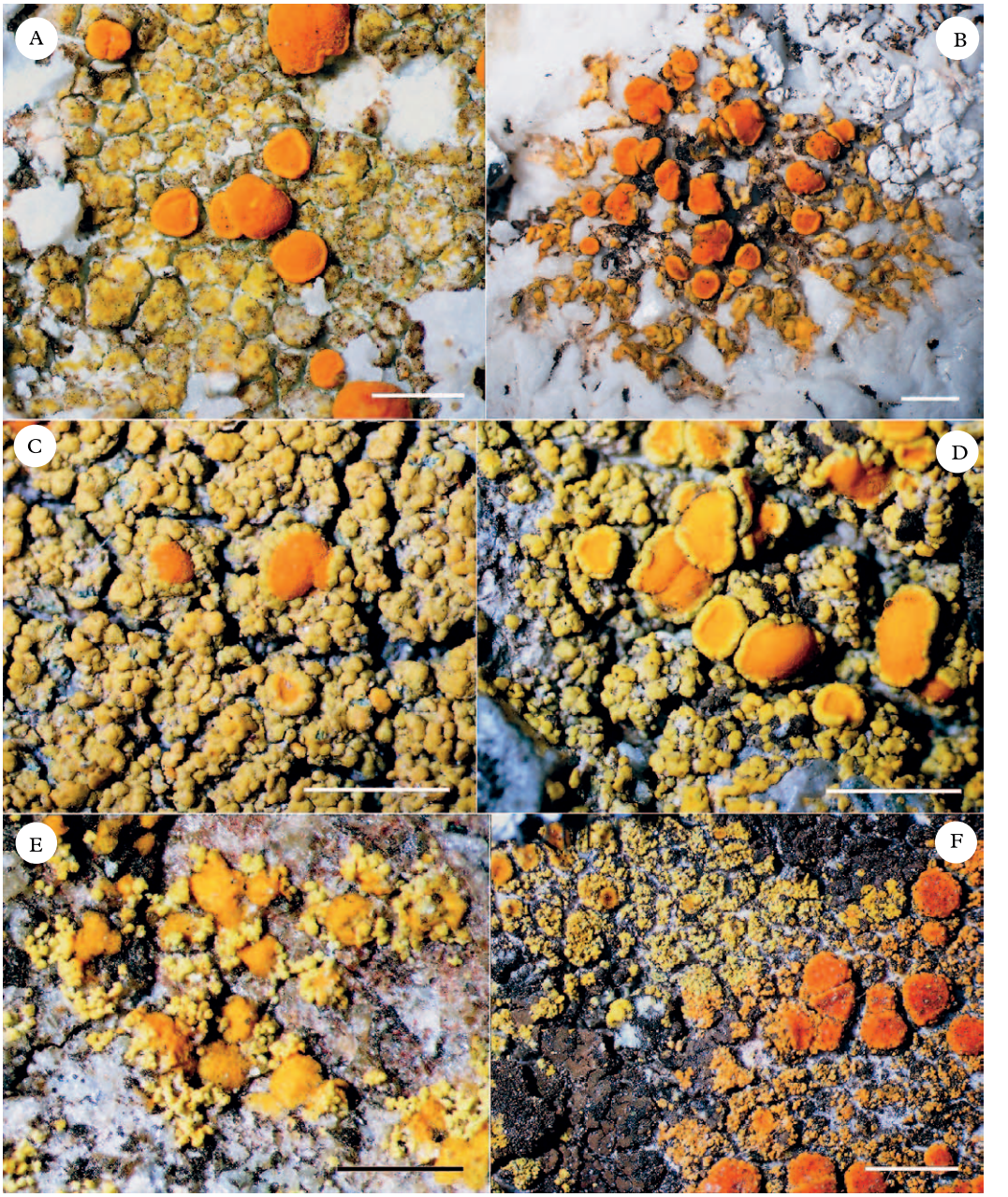


FIG. 7. Morphology of *Caloplaca* species. A & B, *Caloplaca calcitrapa*; C & D, *C. communis*; E, *C. confusa*; F, *C. dichroa*. Scales: A–F = 1 mm.

(*n* = 15); epinecral layer usually with intermixed crystals.

Apothecia frequent, (0·28–) 0·46 ± 0·15 (–0·75) mm diam. (*n* = 20). Disc flat to strongly convex in old apothecia. *Exciple* (40–) 100 ± 34 (–210) µm thick (*n* = 57), zeorine, the true exciple/thalline exciple ratio very variable; thalline exciple enlarged with

age. *Hymenium* (60–) 68 ± 6 (–80) µm thick (*n* = 15). Paraphyses tips widened to (4·0–) 5·5 ± 0·75 (–7·0) µm (*n* = 25). *Ascospores* (7·0–) 11·0 ± 2·0 (–14·0) × (4·5–) 6·0 ± 0·75 (–7·5) µm (*n* = 32); length/breadth ratio *c.* 1·83. *Ascospores* usually thin-walled (in the Black Sea region); thick-walled, sand-clock spores observed only in two samples. Ascospore septa (3·0–) 4·5 ± 1·0 (–6·5) µm thick (*n* = 32), *c.* 0·4 of ascospore length.

Conidia (2·5–) 3·3 ± 0·4 (–4·0) × (1·0–) 1·3 ± 0·25 (–1·5) µm (*n* = 15).

Remarks. According to Navarro-Rosinés *et al*. (2000), the species is characterized mainly by thick-walled, sand-clock ascospores, but these were only rarely observed in specimens from the Black Sea and Marmara Sea regions (CBFS JV6109 & JV6112). More common forms with thin-walled spores were confirmed by the DNA analysis (CBFS JV3408, JV5486 & JV6100).

The areolate or bullate thallus of *Caloplaca calcitrapa* may be confused with the inland and facultatively lichenicolous species *C. inconnexa*, but *C. calcitrapa* seems to be ± maritime and not lichenicolous.

Phylogeny. The four very divergent ITS sequences of *Caloplaca calcitrapa* form a monophyletic group with good PP support (1·00) but a very poor bootstrap support (BS = 53) in a sister position to a clade including *C. confusa*, *C. marina*, *C. microthallina*, and *C. nigromarina* (PP = 0·91, BS < 50).

Ecology and distribution. In the Black Sea region, the species inhabits strongly calcareous substrata, for example hard limestone and lime-rich schist. In coastal areas, it specifically occurs in the supralittoral zone (Rusalka, Bulgaria, sheltered shore: from 1 m upwards; Kamen Brjag, Bulgaria, exposed shore: from 6 m upwards). In western Mediterranean, it is also known from inland localities (Navarro-Rosinés *et al*. 2000). Accompanying species: *Caloplaca* cf. *aegea*, *C. biatorina* s. lat., *C. decipiens*, *C. erythrocarpa*, *C. ferrarii*, *C. limonia*, *C. navasiana*, *Candelariella aurella*, *Diplotomma alboatrum* s. lat., *Lecanora albescens*, *L. campestris*, *L. dispersa*, *Rinodina gennarii*, *Verrucaria nigrescens*, and *Xanthoria* cf. *calcicola*. The species is known from Algeria, France, Italy, Morrocco and Spain (Navarro-Rosinés *et al*. 2000, Roux et al. 2003). It is recorded here for the first time from Bulgaria, Turkey and Ukraine.

Specimens examined. **Bulgaria:** *Black Sea coast*: Kavarna, limestone cliffs on seashore 1·5 km NE of Kamen Brjag, 2007, *J. Vondrák* (CBFS JV5486, 6117, 6130).—**Turkey:** *Black Sea coast*: Istanbul, Kemerburgaz, Karaburun, 2005, *J. Vondrák* (CBFS JV3408); Kandıra, coastal limestone rocks 6 km E of Cebeci, 2007, *J. Vondrák* (CBFS JV6112); *Marmara Sea coast*: Armutlu, coastal rocks 5·5 km SW of Esenköy, 2007, *J. Vondrák* (CBFS JV6100, 6109); Bandırma, coastal rocks near Yenice, 2007, *J. Vondrák* (CBFS JV6118, 6123, 6125, 6129, 6180); Gallipoli Peninsula, coastal limestone cliffs 1 km NE of Abide monument, 2007, *J. Vondrák* (CBFS JV6103).—**Ukraine:** *Crimean Peninsula*: Sudak, coastal rocks at W part of Cape Meganom, 2007, *J. Vondrák* (CBFS JV5906); Sea of Azov coast, 1995, *A. Redchenko* (KHER 2986, sub *C. marina*).

Caloplaca communis Vondrák, Říha, Arup & Søchting sp. nov.

Caloplaca calcitrapae et *maritimae* similis, differt superficie thalli grosse granulato granulis (70–) 180 ± 66 (–380) µm latis. Habitat in rupibus maritimis tantum praecipue silcieis.

Typus: Bulgaria, The Black Sea coast, Burgas, Tsarevo, coastal rocks SE of town, near small boat-factory, 42°08′49.7″N, 27°52′48.2″E, on siliceous rock in supralittoral zone, 30 November 2005, *J. Vondrák* (CBFS JV4620—holotypus; isotypi will be distributed in J. Vondrák*: Sel. Exs. Caloplaca*, fasc. 2).

(Fig. 7C & D)

Thallus yellow (with orange tint in populations from Crete) areolate, bullate to minutely squamulose. Areoles dispersed or contiguous and then overgrowing each other, forming thick crusts in luxuriant populations, (90–) 190 ± 75 (–450) µm thick (*n* = 53) and (0·32–) 0·86 ± 0·43 (–2·8) mm wide (*n* = 121). When the thallus is well-developed, its surface is coarsely granular; granules (70–) 180 ± 66 (–380) µm diam. (*n* = 135). *Cortex* present, (5–) 17 ± 7·5 (–46) µm thick (*n* = 134).

Apothecia frequent, (0·2–) 0·6 ± 0·2 (–1·3) mm diam. (*n* = 97). Disc in mature apothecia slightly concave to flat, never distinctly

convex. *Exciple* (40–) 100 ± 34 (–210) µm thick (n = 57), often crenulate; true exciple fills *c.* ⅓–½ of the exciple width, thalline exciple prominent. *Hymenium* (50–) 68 ± 12 (–100) µm thick (n = 48). *Paraphyses* tips widened to (3·0–) 5·0 ± 1·0 (–7·0) µm (n = 80). *Ascospores* (10·0–) 13·0 ± 1·5 (–18·0) × (4·0–) 6·5 ± 1·0 (–9·0) µm (n = 78); length/breadth ratio *c.* 2·0. Ascospore septa (3·0–) 5·0 ± 1·0 (–7·0) µm thick (n = 78), *c.* 0·4 of ascospore length.

Conidia (2·0–) 2·8 ± 0·3 (–3·5) × (1·0–) 1·2 ± 0·2 (–2·0) µm (n = 52).

Etymology. The name reflects a *common* occurrence of this species on siliceous seashore cliffs.

Remarks. The yellow thallus, covered by coarse granules, together with its occurrence restricted to coastal habitats (mainly siliceous rocks), are the main characters distinguishing *Caloplaca communis* from the similar *C. calcitrapa* and *C. inconnexa*. Nevertheless, some morphotypes of *C. communis* have a thallus with an indistinctly granular surface and if such a morphotype occurs on a calcareous substratum then it is hardly distinguishable from the likewise coastal *C. calcitrapa*. When the areoles/squamules are dispersed, *C. communis* may resemble the North and West European *C. microthallina*, but this species has smaller squamules, 0·3–0·5(–1·0) mm wide (Arup 1994). Morphotypes with a more compact thallus and a less distinct granular surface resemble *C. maritima*, which is not confirmed from the region. *Caloplaca ora*, which is a heterogenous taxon, is another similar 'species', but with a typically orange-red thallus without a granular surface.

Phylogeny. All the sequences sampled of *C. communis* except one form a monophyletic group in the molecular analysis but with low support (PP = 0·87, BS < 50)). The position of the remaining sequence assigned to this species (EU563409) is controversial, appearing in a polytomy between *C. communis*, *C. maritima* and *C. ora* p. p. As in the case of *C. austrocitrina*, sampling of more loci could possibly make parts of the molecular tree more consistent. The genetic affinity of *C. maritima* and *C. ora* p. p. to *C. communis* is, however rather strong (PP = 0·99, BS = 78).

Ecology and distribution. *Caloplaca communis* is one of the commonest species in the lichen communities of the lower supralittoral zone on hard siliceous rocks. Only very rarely, it occurs on sandstone, claystone and limestone cliffs. The species is restricted to a narrow zone close to sea level; sheltered shores: 2–4 m (Tuapse, Russia), 1–2 m (Kiten, Bulgaria); exposed shores: 3–7 m (Sarp, Turkey), 4–17 m (Bulgaria, Rezovo) and 4–19 m (Sinop, Turkey). In the eastern Mediterranean, where the salinity is higher and the climate warmer and drier, the species may occur higher above sea level: *c.* 20–50 m (Agia Pelagia, northern Crete) and *c.* 100 m (Kali Limenes, southern Crete). Accompanying species: *Amandinea punctata*, *Caloplaca* cf. *aegea*, *C. confusa*, *C. fuscoatroides*, *C. limonia*, *Lecanora campestris*, *Rinodina confragosa*, *R. gennarii*. It is widely distributed in the Black Sea region, Marmara Sea and in the eastern Mediterranean. It is known from Bulgaria, Greece, Italy, Russia, Turkey and Ukraine.

Specimens examined: **Bulgaria:** *Black Sea coast*: Burgas, Kiten, 2007, *J. Vondrák* (CBFS JV6088); Burgas, Sozopol, 2007, *J. Vondrák* (CBFS JV6121); Burgas, Tsarevo, 2005, *J. Vondrák* (CBFS JV3369); Burgas, Tsarevo, Rezovo, 2005, *J. Vondrák* (CBFS JV3043).—**Greece:** *Crete*: Ano Viannos, Sidonia, 2005, *J. Vondrák* (CBFS JV4114); Iraklio, Agia Pelagia, 2005, *J. Vondrák* (CBFS JV3803, 3836); Mires, Kali Limenes, 2005, *J. Vondrák* (CBFS JV3763).—**Italy:** *Sardinia*: Planargia, 1983, *W. Brunnbauer* (W, sub *C. microthallina*).—**Russia:** *Black Sea coast*: Tuapse, coastal rocks NW of town, Tuapse, 2007, *J. Vondrák* (CBFS JV6108). *Sea of Azov coast*: Taman Peninsula, clay coast 4·5 km NW of Kuchugury, 2007, *J. Vondrák* (CBFS JV6104).—**Turkey:** *Black Sea coast*: Amasra, coastal rocks near Çakrazboz, 2007, *J. Vondrák* (CBFS JV6127); Cide, coastal rocks near Denizkonak, 2007, *J. Vondrák* (CBFS JV6115); Istanbul, Kemerburgaz, Kilyos, 2005, *J. Vondrák* (CBFS JV3367, 3467, 3471, 3472); Kandıra, sand dunes and coastal limestone rocks 6 km E of Cebeci, 2007, *J. Vondrák* (CBFS JV6119); Lülenburgaz, Demirköy, Limanköy, 2005, *J. Vondrák* (CBFS JV3037); Lülenburgaz, Vize, Kiyiköy, 2005, *J. Vondrák* (CBFS JV3042); Ordu, coastal rocks near Mersin, 2007, *J. Vondrák* (CBFS JV6128); Zonguldak,

coastal rocks near Ilıksu, 2007, *J. Vondrák* (CBFS JV6116). *Marmara Sea coast*: Armutlu, coastal rocks 5·5 km SW of Esenköy, 2007, *J. Vondrák* (CBFS JV6114); Karabiga, 2007, *J. Vondrák* (CBFS JV6110, 6111, 6124).—**Ukraine:** *Crimean Peninsula*: Cape Alushtinska miska, 2000, *A. Khodosovtsev* (KHER 2979, sub *C. microthallina*); Cape Meganom, 1999 & 2002, *A. Khodosovtsev* (KHER 2977, 2980, 2981, sub *C. microthallina*); Cape Plaka, 1999, *A. Khodosovtsev* (KHER 2982, sub *C. microthallina*); Karadag, 2000, *A. Khodosovtsev* (KHER 2976, sub *C. microthallina*).

Caloplaca confusa Vondrák, Říha, Arup & Søchting sp. nov.

Caloplaca flavocitrinae et *nigromarinae* similis, differt praesentia soraliorum typo *C. confusae*, *flavocitrinae* et *limoniae*. Habitat in rupibus maritimis silcieis tantum.

Typus: Bulgaria, Black Sea coast, Burgas, Kiten, rocks near mouth of Karaagach river S of town, 42°13′31.26″N, 27°46′40.46″E, on coastal, base-rich, siliceous rock, 9 April 2007, *J. Vondrák* (CBFS JV6206—holotypus; BM, C, GZU, LD—isotypi). ITS sequence of the holotypus: EU563449.

(Fig. 7E)

Thallus yellow to yellow-orange, of dispersed squamules, or continuous, areolate. Areoles/squamules (80–) 121 ± 28 (–180) μm thick (n = 16) and (0·2–) 065 ± 0·3 (–1·4) mm wide (n = 34). Areoles and squamules flat, smooth or covered by blastidia, with laminal or marginal soralia of *confusa*, *flavocitrina* or *limonia* type; soredia (18–) 31 ± 9 (–43) μm diam. (n = 28), sometimes gathered to small consoredia. Cortex poorly developed; alveolate cortex (7–) 18 ± 8·5 (–40) μm thick (n = 15).

Apothecia infrequent (25% of samples fertile), *c.* 04–1·0 mm in size (n = 7). Discs observed in mature apothecia ± flat. *Exciple* 50–110 μm thick (n = 7), zeorine, but appearing biatorine; in young apothecia, the true exciple fills the whole exciple width, as the thalline exciple is hidden below the true exciple. *Hymenium* 70–80 μm thick (n = 9). *Paraphyses* tips widened to (3·5–) 4·5 ± 0·5 (–5·5) μm (n = 18). *Ascospores* (10·0–) 11·5 ± 1·0 (–13·0) × (4·5–) 5·5 ± 1·0 (–7·0) μm (n = 17); length/breadth ratio *c.* 2·1. Ascospore septa (3·5–) 5·0 ± 1·0 (–7·0) μm thick (n = 17), *c.* 0·43 of ascospore length.

Conidia c. 3–3·5 × 1–1·5 μm.

Etymology. The name expresses the confusing position of the new species in the phylogenetic tree; although very similar to *Caloplaca flavocitrina* and *C. nigromarina*, it is not closely related to them.

Remarks. This species may be characterized by its squamulose to areolate thallus with all three types of soralia (*confusa*, *flavocitrina* and *limonia* types), but in some cases, it is indistinguishable from *Caloplaca flavocitrina* and *C. nigromarina*.

Phylogeny. The sequences of *Caloplaca confusa* form a monophyletic group, but the support is not very strong (PP = 0·89, BS = 46). However, it is morphologically distinct from its genetically closest relative, *C. microthallina*, in the analyses. The support for this sister relationship is not very strong (PP = 0·88, BS = 47).

Ecology and distribution. *Caloplaca confusa* is restricted to hard siliceous, mainly volcanic, sea shore cliffs in the supralittoral zone; from *c.* 2 m upwards in sheltered shores and 5–18 m on an exposed shore (Sinop, Turkey). Accompanying species: *Caloplaca* cf. *aegea*, *C. communis*, *C.* cf. *holocarpa*, *C. limonia*, *C. thracopontica*, *Catillaria chalybeia*, *Hyperphyscia adglutinata*, *Lecania* cf. *aipospila*, *Lecanora campestris*, *L. dispersa*, *L.* cf. *salina*, *Rinodina gennarii*, and *Xanthoria* cf. *calcicola*.

It is probably widely distributed in the Black Sea region and the Mediterranean, and is also known from the Atlantic coast. Records from Azores, Bulgaria, France and Italy are confirmed by molecular data. There are also collections from Georgia, Russia, Turkey and Ukraine, but these were not confirmed by molecular data and have been omitted from this study.

Specimens confirmed by ITS data. **Bulgaria:** *Black Sea coast*: Burgas, Tsarevo, coastal rocks between Tsarevo and Ahtopol, 2005, *J. Vondrák* (CBFS JV3435).—**France:** *Corsica*: Ajaccio, on volcanic rock in alt. 50 m, 1993, *J. Hafellner* (GZU, sub *C. citrina*).—**Italy:** *Sicily*: Isole Pelagie, Linosa, 1992, *J. Poelt* (GZU, sub *C. citrina*).—**Portugal:** *Azores*: Sao Jorje, 1992, *F. Berger* (hb. Berger).

Caloplaca dichroa Arup

Lichenologist **38:** 13 (2006); type: Sweden, Västergötland, Klefva infra Mösseberg. In saxis calcaris, 1914, *Vrang.* Malme: *Lichenes suecici exsiccati* 525 (LD—holotype).

(Fig. 7F)

Thallus areolate, of two colour forms, yellow and orange. Areoles (70–) 118 ± 36 (–210) μm thick (n = 19) and (0·24–) 0·6 ± 0.·3 (–1.·2) mm wide (n = 20), ± entirely covered by blastidia/soredia of *limonia* type, (23–) 40 ± 11 (–61) μm diam. (n = 30). *Cortex* indistinct, composed of 1–2 layers of cells; a thicker alveolate cortex developed in spots.

Apothecia frequent, (0·42–) 0·49 ± 0·06 (–0·64) mm (n = 15). Disc in mature apothecia slightly concave to slightly convex. *Exciple* (50–) 83 ± 18 (–110) μm thick (n = 15), zeorine, the true exciple/thalline exciple ratio very variable; thalline exciple often covered by blastidia/soredia, enlarged with age. *Hymenium c.* 70–80 μm thick (n = 5). *Paraphyses* tips swollen up to (2·5–) 4·5 ± 1·0 (–6·0) μm (n = 34). *Ascospores* thick-walled (walls up to 2 μm) or thin-walled (walls less than 0·5 μm), (11·0–) 14·0 ± 1·5 (–16·0) × (6·0–) 7·25 ± 0·75 (–9·0) μm (n = 15); length / width ratio *c.* 1·93. Ascospore septa (3·5–) 4·0 ± 0·4 (–4·5) μm thick (n = 15), *c.* 0·29 of ascospore length.

Conidia (1·5–) 2·5 ± 0·5 (–3·0) × (1·0–) 1·25 ± 0·25 (–1·5) μm (n = 20).

Remarks. The species is characterized by its sorediate/blastidiate thallus surface, *limonia* type of soralia and thin thallus without marginal lobes. The yellow and orange thallus forms, often growing side by side, are also diagnostic. It can be confused with *Caloplaca austrocitrina* and *C. limonia*, but the former has a generally thicker thallus and a different type of soralium, and the latter has a thicker thallus, larger vegetative diaspores and lacks the orange morphotype. For differences from *C. citrina* and *C. coronata* see Arup (2006*a*). The thick-walled ascospores seem to be diagnostic in the Nordic coutries (Arup 2006*a*), but in the Black Sea region some specimens have thin-walled spores. A similar pattern has also been observed in some British specimens.

Phylogeny. *Caloplaca dichroa* forms one of the best-supported clades in our analysis; it has full support (PP = 1·00, BS = 100). This branch appears as a sister taxon to a clade of *C. arcis, C. arcisproxima* and *C. limonia* with fairly good support in the Bayesian analysis (PP = 0·93).

Ecology and distribution. Although this species is known also from concrete and mortar (Arup 2006*a*; Vondrák *et al.* 2007), in the Black Sea region, it has only been collected from ± sun-exposed, hard or soft calcareous stones or cliffs. It is a typical inland species avoiding maritime conditions; on coastal cliffs it grows from 6 m upwards on sheltered shores (Rusalka, Bulgaria) and from 16 m and upwards on more exposed shores (Kamen Brjag, Bulgaria). Accompanying species: *Candelariella aurella*, *C. rhodax*, *Lecanora albescens*, *L. dispersa*, *Phaeophyscia nigricans*, *P. orbicularis*, *Physcia adscendens*, *Physconia grisea*, *Verrucaria macrostoma* f. *furfuracea*, and *V. nigrescens* s. lat.

Selected specimens examined. **Austria:** *Styria*: Eisenerzer Alpen, Kammern im Liesingtal, 1997, *J. & A. Hafellner* (GZU, sub *C. citrina*); Grazer Bergland, Mixnitz, alt. 1620 m, 2005, *J. Hafellner* (GZU, sub *C. citrina*); Fischbacher Alpen, Rettenegg, 2002, *J. Hafellner* (GZU, sub *C. citrina*). *Tirolia*: Hohe Tauern Mts, Matrei, alt. 1000 m, 1998, *J. Hafellner* (GZU, sub *C. citrina*).—**Bulgaria:** Kavarna, Cape Kaliakra, 2007, *J. Vondrák* (CBFS JV6177).—**Great Britain:** *England*: **V. C. 34,** West Gloucestershire: Bristol, rocks on right side of Avon River near Clifton suspension bridge, 2006, *J. Vondrák* (CBFS JV4155).—**Hungary:** *Mt Bakony*: Hárskut, 1968, *K. Verseghy* (BP 75193, 75204).—**Romania:** *Dobrogea*: Jurilovca, rocky cliff at Doloşman Cape, 2007, *J. Vondrák* (CBFS JV5324, 5337); Tulcea, Popina Island (Insula Popina) in Razim Lake (Lacul Razim), 2007, *J. Vondrák* (CBFS JV6178, 6179).—**Russia:** *Sea of Azov coast*: Taman Peninsula, on soft limestone, 4·5 km NW of Kuchugury, 2007, *J. Vondrák* (CBFS JV6176).—**Ukraine:** *Crimean Peninsula*: Feodosia, Karadag, near village Kurortnoye, 2007, *J. Vondrák* (CBFS JV5477).

Caloplaca flavocitrina (Nyl.) H. Olivier

Lich. d'Europe **2:** 110 (1908–1910).

Lecanora flavocitrina Nyl., *Flora* **69:** 461 (1886); type: Great Britain, Staveley, 1886, *Martindale* (H-Nyl.!, lectotype selected by Wade 1965).

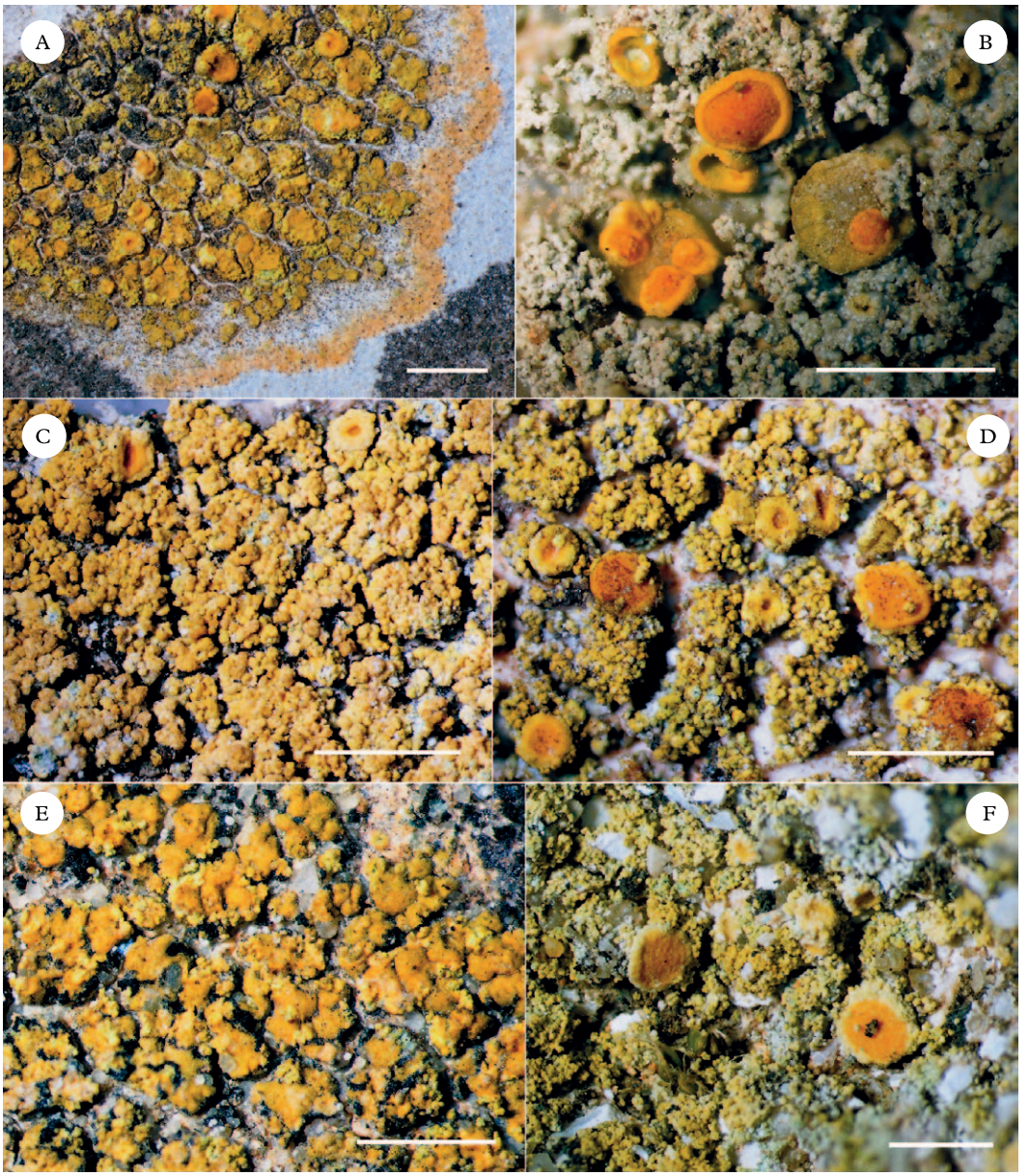


FIG. 8. Morphology of *Caloplaca* species. A, *Caloplaca flavocitrina*; B, *C. geleverjae*; C & D, *C. limonia*; E, *C. nigromarina*; F, *C. phlogina*. Scales: A–F = 1 mm.

(Fig. 8A)

Thallus yellow, of dispersed squamules, rarely continuous, areolate. Squamules (70–) 96 ± 17 (–140) µm thick (n = 16) and (0·12–) 0·4 ± 0·17 (–0·75) mm wide (n = 60). Squamules flat, smooth, with marginal soralia of *flavocitrina* type, but the soralia sometimes expand and cover the complete surface of the squamules. Soredia (16–) 29 ± 9 (–65) µm diam. (n = 56), sometimes gathered into consoredia. *Cortex* thin,

usually of 1–2 layers of cells; alveolate cortex (4–) 9 ± 5 (–25) µm thick (n = 44). A white or yellow fibrillar prothallus was observed on smooth substrata.

Apothecia infrequent (30% of samples fertile), (0·3–) 0·43 ± 0·1 (–0·75) mm diam. (n = 24). Disc in mature apothecia slightly concave to flat. *Exciple* (70–) 85 ± 13 (–110) µm thick (n = 16), zeorine, the true exciple/thalline exciple ratio very variable; thalline exciple enlarged with age. *Hymenium* (65–) 75 ± 6 (–80) µm thick (n = 14). *Paraphyses* tips swollen to (3·0–) 5·0 ± 1·0 (–7·0) µm (n = 32). *Ascospores* (10·0–) 11·5 ± 1·25 (–14·5) × (4·0–) 5·5 ± 1·0 (–7·0) µm (n = 27); length/width ratio *c.* 2·1. Ascospore septa (3·0–) 4·5 ± 1·0 (–7·0) µm thick (n = 27), *c.* 0·39 of ascospore length.

Conidia (2·0–) 3·25 ± 0·5 (–4·0) × (1·0–) 1·15 ± 0·25 (–1·5) µm (n = 14).

Remarks. This species has a squamulose to areolate thallus with mainly *flavocitrina* type of soralium. It is hardly distinguishable from *C. confusa* and *C. nigromarina*, but its thallus is usually yellow and the *flavocitrina* type of soralium persists. It differs also in its ecology, being mainly an inland species, and is rather rare on sea-shore rocks.

Phylogeny. The sequences of *Caloplaca flavocitrina* form a well-supported monophyletic group in the Bayesian analysis (PP = 0·99), but the parsimonious analysis gave a weaker support (BS = 61). Together with *C. geleverjae* and an undescribed taxon, represented by the sequence EU563389, it forms a well supported clade (PP = 1·00, BS = 89), that appears as a sister group to a large clade with, for example, *C. dichroa* and *C. arcis*, but with rather poor support (PP = 0·84, BS < 50).

Ecology and distribution. *Caloplaca flavocitrina* is one of the ecologically broadest species in the *C. citrina* group; it occurs on bark, wood, concrete and on a variety of rocks. In maritime conditions, it is mainly restricted to concrete or calcareous rocks. It is confirmed from siliceous coastal cliffs only in the most humid part of the Black Sea region in Georgia and NE Turkey. Accompanying species in coastal localities: *Caloplaca albolutescens*, *Candelariella aurella*, *Diplotomma alboatrum* s. lat., *Lecanora dispersa*, *Rinodina gennarii*, and *Verrucaria macrostoma* f. *furfuracea*.

As it is known throughout Europe and from the Hawaiian Islands, it may have a circumpolar distribution. It is a new record for Georgia, Italy, Russia, and Turkey.

Specimens confirmed by ITS nrDNA data. **Bulgaria:** *Black Sea coast*: Burgas, Pomorie, on concrete, 2005, *J. Vondrák* (CBFS JV3425); Burgas, Tsarevo, Sinemorec, epiphytic, 2004, *J. Vondrák* (CBFS JV2106).—**Georgia:** *Adjara*: Batumi, valley of river Acharistskali near Shuakhevi, 2007, *J. Vondrák* (CBFS JV6094); Batumi, rocks near coast on S periphery of Gonio, 2007, *J. Vondrák* (CBFS JV6098).—**Italy:** Livorno, volcanic coastal rock, alt. 20–50 m, 1993, *J. Hafellner* (GZU, sub *C. citrina*).—**Russia:** *Black Sea coast*: Gelendzhik, coastal rocks W of Krinitsa (near Betta), 2007, *J. Vondrák* (CBFS JV6089); Sochi, coast 2 km SE of Loo, 2007, *J. Vondrák* (CBFS JV6095).—**Turkey:** *Black Sea coast*: Rize, coastal outcrops close to city, 2007, *J. Vondrák* (CBFS JV6090).—**USA:** *Hawaii*: Maui, Haleakala, volcanic rock, alt. 1700 m, 1996, *C. Wetmore* (GZU, sub *C. citrina*).

Caloplaca geleverjae Khodosovtsev & S. Kondr.

Ukr. Botan. Journ. **60:** 294 (2003); type: Ukraine, Crimea AR, Feodosia region, cape Meganom, on conglomerates in supralittoral zone, 2002, *A. Khodosovtsev* (KW—holotype; KHER!, CBFS!—isotypes). ITS sequence of a topotype: EU563423.

(Fig. 8B)

Thallus pale grey, rarely yellowish (mainly at apothecial primordia), consisting of dispersed or continuous areoles, areolate. Areoles (110–) 147 ± 18 (–180) µm thick (n = 15) and (0·34–) 0·63 ± 0·16 (–0·87) mm wide (n = 15). Squamules ± entirely covered by blastidia, (48–) 85 ± 31 (–148) µm diam. (n = 15); true soredia absent. Cortex indistinct; alveolate cortex (18–) 28 ± 9 (–50) µm thick (n = 15).

Apothecia frequent in the known population, (0·37–) 0·48 ± 0·07 (–0·62) mm diam. (n = 15). Disc in mature apothecia slightly concave to flat. *Exciple* (70–) 93 ± 14 (–110) µm thick (n = 14), zeorine, but thalline exciple hidden below the true exciple in

young apothecia. *Hymenium c.* 60–80 µm thick (*n* = 5). *Paraphyses* tips swollen to (5·0–) 6·0 ± 0·75 (–7·0) µm (*n* = 15). *Ascospores* (10·0–) 13·25 ± 1·5 (–15·0) × (5·0–) 6·5 ± 1·0 (–8·0) µm (*n* = 15); length/breadth ratio *c.* 2·04. Ascospore septa (3·0–) 4·75 ± 0·75 (–6·0) µm thick (*n* = 15), *c.* 0·36 of ascospore length.

Conidia (2·5–) 3·0 ± 0·4 (–3·5) × (1·0–) 1·3 ± 0·2 (–1·5) µm (*n* = 15).

Remarks. The predominantly greyish thallus colour distinguishes *Caloplaca geleverjae* from other related species. The blastidiate species, *Caloplaca thamnoblasta*, is somewhat similar in thallus structure, but its thallus is usually yellow and it does not belong to the *C. citrina* group (J. Vondrák & J. Šoun, unpublished molecular data).

Phylogeny. *Caloplaca geleverjae* (one sequence included in the analysis) is a sister species to *C. flavocitrina* (PP = 0·98; BS = 60).

Ecology and distribution. Caloplaca geleverjae is known only from the type locality in the Crimean Peninsula, where it occurs on ± shaded, base-rich conglomerate in the lower supralittoral zone, at altitudes below 10 m. The accompanying species in the type locality were few and included for example, *Caloplaca limonia* and *C.* cf. *nigromarina*.

Specimen examined. **Ukraine:** *Crimean Peninsula*: Cape Meganom, 2007, *J. Vondrák & A. Khodosovtsev* (CBFS JV5415—topotype).

Caloplaca limonia Nimis & Poelt

in Nimis, Poelt, Tretiach, Ottonello, Puntillo & Vězda, *Bull. Soc. Linn. Provence* **45:** 252 (1994); type: Italy, Isole Egadi, Marettimo, 1991, *J. Poelt* (GZU!—holotype). ITS sequence of a paratype: EU563467.

(Fig. 8C & D)

Thallus dull to bright yellow, often white-pruinose, forming a continuous areolate crust. Areoles/squamules (100–) 248 ± 111 (–550) µm thick (*n* = 44) and (0·18–) 0·98 ± 0·51 (–2·6) mm wide (*n* = 140). Areoles and squamules flat, covered by blastidia or by laminal soralia of *limonia* type; soredia/blastidia (26–) 85 ± 54 (–320) µm diam. (*n* = 138). *Cortex*/alveolate cortex (4–) 15 ± 10 (–55) µm thick (*n* = 109).

Apothecia frequent, *c.* (0·25–) 0·6 ± 0·25 (–1·6) mm diam. (*n* = 114). Disc in mature apothecia slightly concave to flat. *Exciple* (70–) 121 ± 31 (–200) µm thick (*n* = 25), zeorine, thalline exciple prevailing in old apothecia, sometimes covered by blastidia/isidia. *Hymenium* (60–) 78 ± 17 (–130) µm thick (*n* = 50). *Paraphyses* tips widened to (3·0–) 4·5 ± 0·5 (–6·0) µm (*n* = 72). *Ascospores* (9·0–) 13·0 ± 1·5 (–16·0) × (3·0–) 6·5 ± 1·0 (–9·0) µm (*n* = 77); length/breadth ratio *c.* 2·0. Ascospore septa (3·0–) 5·5 ± 1·0 (–8·0) µm thick (*n* = 77), *c.* 0·42 of ascospore length.

Conidia (2·5–) 3·5 ± 0·8 (–5·5) × (1·0–) 1·15 ± 0·25 (–1·5) µm (*n* = 33).

Remarks. The diagnostic characters of this species are large soredia/blastidia, *limonia* type of soralium, ± pale yellow thallus and a thick apothecial margin often covered by blastidia/isidia. *Caloplaca citrina*, that has a more northern distribution, is probably the most similar species, but it differs on average in the smaller vegetative diaspores, which are often blastidia and not soredia.

Phylogeny. The sequences of *Caloplaca limonia* form a well-supported monophyletic group (PP = 1·00, BS = 94). It appears to be related to *C. arcis* along with *C. arcisproxima* (PP = 0·80, BS < 50) and more distantly to *C. austrocitrina* (PP = 0·92, BS < 50).

Ecology and distribution. Caloplaca limonia occurs mainly on coastal calcareous rocks or on base-rich, hard siliceous cliffs in dry sun-exposed to shaded and damp situations, but also on twigs of maritime shrubs or on soil. It is also known from inland localities, but it is often abundant in maritime habitats, where it occurs on sheltered shores from 2 m upwards (Rusalka, Bulgaria); on exposed shores from 20 m (Sinop, Turkey) and 21 m (Rezovo, Bulgaria). Accompanying species: *Caloplaca* cf. *aegea*, *C. albolutescens*, *C. communis*, *C. confusa*, *C. flavescens*, *Caloplaca thracopontica*,

Catillaria chalybeia, *Diploicia canescens*, *Diplotomma alboatrum* s. lat., *Lecanora albescens*, *L. dispersa*, *Physcia adscendens*, *Rinodina gennarii*, *R. pityrea*, *Verrucaria macrostoma* f. *furfuracea*, and *V. nigrescens* s. lat.

Caloplaca limonia is so far reported from Greece (Sipman & Raus 2002), Italy (e.g. Nimis *et al*. 1994) and Ukraine (Khodosovtsev 2001), but it is a common species in the Mediterranean and the Black Sea region. New record for Bulgaria, Croatia, Czech Republic, Georgia, Morrocco, Romania, Russia, and Turkey.

Selected specimens examined. **Bulgaria:** *Black Sea* coast: Kavarna, limestone cliffs on seashore 1·5 km NE of Kamen Brjag, 2007, *J. Vondrák* (CBFS JV6138).—**Croatia:** *Island of Arbe*: Arbe, 1927, *J. B. Kümmerte* (BP 27347).—**Czech Republic:** *South Bohemia*: Písek, in town, 2005, *J. Vondrák* (CBFS JV2515).—**Georgia:** *Black Sea coast*: Batumi, Sarpi (Georgian-Turkish border), 2007, *J. Vondrák* (CBFS JV6150).—**Italy:** Distr. Verona, *Massalongo* (BP 27353, ex hb. A. Massal.).—**Morocco:** Rabat, 1930, *Andreánszky* (BP 46517).—**Romania:** *Dobrogea*. Tulcea, Jurilovca, rocky cliff at Dolosman Cape, 2007, *J. Vondrák* (CBFS JV5376).—**Russia:** *Black Sea coast*: Tuapse, coastal rocks NW of town, 2007, *J. Vondrák* (CBFS JV6160).—**Turkey:** *Black Sea coast*: Sinop, coastal rocks on E coast of peninsula, 2007, *J. Vondrák* (CBFS JV6143). *Aegean Sea coast*: Gallipoli Peninsula, coastal rocks near Güneyli, 2007, *J. Vondrák* (CBFS JV6148). *Marmara Sea coast*: Karabiga, S-exposed coastal rocks on headland E of town, 2007, *J. Vondrák* (CBFS JV6147).—**Ukraine:** *Crimean Peninsula*: Sudak, coastal rocks at W part of Cape Meganom, 2007, *J. Vondrák* (CBFS JV6019).

Caloplaca nigromarina Vondrák, Říha, Arup & Søchting sp. nov.

Similis *Caloplaca flavocitrinae*, differt squamulis plerumque laetius flavo-aurantiacis; a *C. confusae* differt praesentia soraliorum typo *C. confusae* et *flavocitrinae* tantum. Habitat in rupibus maritimis silcieis tantum.

Typus: Georgia**,** Adjar,. Sarpi (Georgian-Turkish border), coastal cliffs N of village, 41°31′58.19″N, 41°32′58.35″E, on siliceous rock, 25 April 2007, *J. Vondrák* (CBFS JV6091—holotypus). ITS sequence of the holotypus: EU563436.

(Fig. 8E)

Thallus yellow-orange (in shaded sites yellow), of dispersed granules/squamules, or thallus continuous, areolate. Areoles/squamules (60–) 106 ± 25 (–170) µm thick (*n* = 39) and (0·18–) 0·44 ± 0·19 (–1·25) mm wide (*n* = 89). Areoles and squamules flat, smooth, with marginal soralia of *confusa* or *flavocitrina* type, soredia/consoredia (16–) 31 ± 9 (–50) µm diam. (*n* = 89). *Cortex* present, (5–) 17 ± 8 (–37) µm thick (*n* = 90).

Apothecia infrequent (40% of specimens fertile), (0·45–) 0·6 ± 0·1 (–0·8) mm diam. (*n* = 15). Disc in mature apothecia flat to slightly convex. *Exciple* (40–) 75 ± 33 (–150) µm thick (*n* = 15), zeorine; true exciple fills *c.* ½ of the exciple width. In young apothecia, thalline exciple may be hidden below the true exciple. *Hymenium* (50–) 70 ± 10 (–90) µm thick (*n* = 13). *Paraphyses* tips widened to (3·0–) 4·5 ± 1·0 (–6·5) µm (*n* = 29). *Ascospores* (9·0–) 11·5 ± 1·5 (–15·0) × (4·0–) 6·0 ± 1·0 (–8·5) µm (*n* = 17); length/breadth ratio *c.* 1·9. Ascospore septa (3·5–) 5·0 ± 1·0 (–7·0) µm thick (*n* = 17), *c.* 0·43 of ascospore length.

Conidia (2·0–) 3·2 ± 0·5 (–4·5) × (1·0–) 1·25 ± 0·25 (–1·5) µm (*n* = 29).

Etymology. The name is derived from the distribution of the new species on shores of the Black Sea.

Phylogeny. The sequences of *Caloplaca nigromarina* form a fairly well-supported monophyletic group (PP = 0·94, BS = 66). At the base of this clade there is a single specimen (EU563433) that cannot be assigned to any known species, but it is apparantly related to *C. nigromarina* (PP = 1·0, BS = 84). However, it differs clearly in its morphology. These two taxa form a sister group to a clade consisting of *C. confusa*, *C. marina* and *C. microthallina* (PP = 0·99, BS = 97).

Remarks. *Caloplaca nigromarina* shares the squamulose thallus and marginal soralia with the very similar species *Caloplaca confusa* and *C. flavocitrina*. However, from the former species, it differs in the *flavocitrina* type of soralia, and from the latter, in the yellow-orange thallus and in ecology.

Ecology and distribution. This species is restricted to siliceous seashore cliffs in the lower supralittoral zone. Accompanying

species are usually few only: for example, *Caloplaca* cf. *aegea*, *C. fuscoatroides*, *Lecanora albescens*, and *L. dispersa*. The species is so far known only from the Bulgarian, Georgian and Turkish Black and Aegean Sea coasts.

Specimens examined. **Bulgaria:** *Black Sea coast*: Burgas, Tsarevo, Sinemorec, coastal rocks, 2004, *J. Vondrák* (CBFS JV4983).—**Turkey:** *Aegean Sea coast*: Gallipoli Peninsula, coastal rocks near Güneyli, 2007, *J. Vondrák* (CBFS JV5482); *Black Sea coast*: Istanbul, Kemerburgaz, Kilyos, 2005, *J. Vondrák* (CBFS JV3354); Lülenburgaz, Vize, Kiyiköy, coastal rocks, 2005, *J. Vondrák* (CBFS JV3035); Zonguldag, Sazköy, 1992, *V. John & E. Sauer* (GZU, *Lich. Anatol. Exsicc.* 80, sub *C. citrina*).

Notes on other species with *Caloplaca citrina* morphology

Caloplaca britannica R. Sant.

in Laundon, *Lichenologist* **24:** 2 (1992); type: Great Britain, Caithness (UPS—holotype; GZU—isotype!).

This taxon was recently misunderstood by Aptroot & van Herk (2004), who considered *Caloplaca britannica* conspecific with *C. limonia*, that is widely distributed in coastal as well as inland Europe; also in the Black Sea region: Crimea (Khodosovtsev 2001, sub *C. limonia*). However, *C. britannica* is a blastidiate-isidiate species that does not belong to the *C. citrina* clade (U. Arup, unpublished) and is restricted to coastal cliffs. We investigated two samples from the Netherlands, named *C. britannica* by A. Aptroot, and both specimens belong to *C. arcis*.

Caloplaca citrina (Hoffm.) Th. Fr.

Acta Soc. Regiae Sci. Upsal. **3:** 218 (1860).—*Verrucaria citrina* Hoffm. *Deutschlands Flora* 198 (1796); type: *Lecanora citrina*, Svecia (H, neotype selected by Nordin 1972).

According to the GBIF web site (www.gbif.org), this species is considered to be cosmopolitan. However, according to molecular data (Arup 2006*a*) and this study, *Caloplaca citrina* may be a species with a rather restricted distribution. The species has so far been confirmed only from North and Central Europe. In the Mediterranean and the Black Sea region it is replaced by other species such as *C. limonia*.

Caloplaca marina (Wedd.) Zahlbr.

in Du Rietz, *Zur Methodologischen Grundlage der Modernen Pflanzenzociologie* 170 (1921).—*Lecanora marina* Wedd., *Mém. Soc. Nat. Sc. Cherb.* **19:** 275 (1875); type: France, Vendée, 1875, *Weddell* (PC—lectotype selected by Nordin 1972; TUR, hb.Vainio 7188—isotypes).

This morphologically distinct species has not been confirmed from the Black Sea region and is probably not present there. Reports from Turkey (John & Breuss 2004) and Ukraine (e.g. Redchenko 2002) are probably incorrect. The Turkish material was not revised by us, but the Ukrainian specimens in KHER (collected by A. Khodosovtsev or A. Redchenko) were identified as *Caloplaca calcitrapa* or *C. irrubescens* (Arnold) Zahlbr.

Caloplaca maritima (B. de Lesd.) B. de Lesd.

Rev. Bryol. Lichénol. **22,** fasc. 3-4**:** 313 (1953).—*Caloplaca citrina* var. *maritima* B. de Lesd., *Sched. ad Krypt. exsicc.*, Cent. 17 (1909); type: France, Dunkerque, on calcareous stone, *B. de Lesdain* (*Krypt. exsicc.* 1667, W!—lectotype selected by Arup 1997*a*).

Based on molecular data, this species is closely related to *Caloplaca communis*. Whereas, *C. communis* occurs in the Black Sea region and the eastern Mediterranean, *C. maritima* is probably restricted to the Atlantic coast of Europe. Samples from southern France named *C. maritima* by Arup (1997*a*), require confirmation. Some specimens of *C. communis* with a smooth thallus without granules are morphologically indistinguishable from well-developed material of *C. maritima* from the Atlantic coast of Europe.

Caloplaca microthallina (Wedd.) Zahlbr.

Cat. Lich. Univ. **7:** 247 (1931).—*Lecanora microthallina* Wedd., *Mém. Soc. Nat. Sc. Cherb.* **19**: 276 (1875); type: France, Vendée, 1875, *Weddell* (PC—lectotype selected by Nordin 1972).

This species may resemble morphologically some morphotypes of *Caloplaca communis* with minute areoles, but *C. microthallina* has not been confirmed from the Black Sea region by molecular data and it is probably absent there. Records from Bulgaria (Vězda 1975) and Ukraine (e.g. Redchenko 2002) are based on *C. communis* and the record from Turkish Eastern Mediterranean (Pišút & Guttová 2008) needs revision.

Caloplaca ora Poelt & Nimis

in Nimis & Poelt, *Studia Geobotanica* **7:** 70 (1987); type: France, Corse, Ajaccio, on granite coastal cliff, 1969, *Lambinon, Rondon & Vězda* (A. Vězda: *Lich. Sel. Exs.* 849, hb. A. Vězda—holotype, W!—isotype).

Based on the samples from GZU and W, we consider this Mediterranean taxon to be heterogeneous. Various specimens with orange, areolate to bullate thalli, otherwise similar to *Caloplaca maritima*, are placed here. However, at least some specimens named as *C. ora*, belong to the *C. citrina* group (Fig. 1). This taxon requires further study.

Caloplaca phlogina (Ach.) Flag.

Mém. Soc. Emulat. Doubs: 250 (1886).—*Parmelia citrina* var. *phlogina* Ach., *Methodus*: 180 (1803); type: Sweden. Skåne: Lund, on *Ulmus*, 2005, *Arup* L05001 (LD!—neotype selected by Arup 2006*a*).

(Fig. 8F)

Although very similar to *Caloplaca citrina*, this species does not belong to the *Caloplaca citrina* clade. The species, known as an epiphyte from northern Europe (Arup 2006*a*) and northern France (Sérusiaux *et al.* 1999), also occurs in the Black Sea region as an epiphyte, but also on loess soil and on concrete.

Specimens confirmed by ITS nrDNA data. **Romania:** Constanta, Mangalia, on concrete, 2005, *Vondrák* (CBFS JV3437, sub *C. citrina*, GenBank nr EU563460).—**Russia:** *Taman Peninsula*: on loess and on *Salicornia* shrubs, 2007, *Vondrák* (CBFS JV6060, 6061, 6224).

General results from the phylogenetic analysis

While this is principally a taxonomic study the results can be considered in a broader context. Some general conclusions and observations are discussed below.

Cryptic or semi-cryptic species.

The results show that there were several unrecognized species among the taxa analyzed. Some of these, for example, *C. communis* and *C. arcisproxima*, can be fairly easily characterized morphologically even if they are similar to other species of the group. Others, such as *C. austrocitrina* and *C. nigromarina*, are very difficult to distinguish morphologically from *C. flavocitrina* and many forms of these species are indistinguishable from each other without molecular analyses. Morphological characters may provide only a hint as to which species the specimen belongs, but there is such a large overlap that these characters are very hard to use. These difficult species are more or less cryptic, but we propose to call them 'semi-cryptic', since there are differences in their ecology and distribution and we feel that there will be a significant loss of information if they are not described.

In addition, the species which are difficult to separate by morphology are not sister species. For example, *C. austrocitrina*, *C. nigromarina* and *C. flavocitrina* belong to three different phylogenetic clades (Fig. 1), mixed with several other species, which are clearly non-cryptic. If one were to lump the similar species into single taxa this would produce polyphyletic taxa, and that would not be acceptable. Therefore, we feel that the semi-cryptic species also need to be formally described. Another example of indistinguishable taxa is *C. citrina* and *C. phlogina*, which sometimes have identical morphology but belong to two separate larger clades.

Cryptic species problems have been recently referred to in several works; probably the best known are studies on phylogenetic species bounderies in *Letharia* (Arnerup *et al.*

2004; Kroken & Taylor 2001). Several 'cryptic species' were revealed in *Letharia*, but some of the species differ slightly in morphology, chemistry and distribution, and could be considered to be 'semi-cryptic'. Similarly, the new species in *Parmelina quercina* s. lat. (Argüello *et al*. 2007) or in *Parmelia saxatilis* s. lat. (Crespo *et al*. 2002) could also be considered to be semi-cryptic. In *Caloplaca*, for example, *C. albopruinosa* and *C. alociza* could be considered semi-cryptic, as they are largely indistinguishable on morphological grounds (Muggia *et al*. 2008).

Convergences

There are strong convergences in morphology in distantly related sorediate species. For example *C. flavogranulosa*, *C. phlogina*, *C. sorediella* and *C. soropelta* are morphologically very similar to some members of the *C. citrina* clade, but belong to different, unrelated groups. It is therefore sometimes not possible to assign a species to the *C. citrina* clade without molecular analyses. Even within this clade there are very similar species placed in distant positions of the phylogenetic tree (Fig. 1).

Changes in vegetative characters

It is surprising how frequent shifts from a sorediate to a non-sorediate state or switches between the different kinds of soralium (*flavocitrina*-type vs. *limonia*-type) seem to have taken place. Whether these shifts are due to mutations or variations in the expression of genes is not known, but it does cause problems in the understanding of the taxonomy. If we assume that the *C. citrina* clade evolved from a non-sorediate ancestor, there has been, for instance a single appearance of soredia followed by four independent losses of soredia.

Biodiversity

The number of species in the *C. citrina* clade will probably increase if this group is surveyed in other geographical areas using molecular data. This is also confirmed by new data from the British Isles (U. Arup, unpublished data).

Species distribution

Some taxa, which were considered to be wide-spread or even cosmopolitan, have in fact very restricted natural ranges. For instance, *C. citrina* s. str. is absent from the Black Sea region and its range may be restricted to only parts of Europe. This same pattern appears to occur for some maritime species, for example, *Caloplaca marina*, *C. maritima*, and *C. microthallina*, which are absent from the Black Sea region and very probably from the eastern Mediterranean.

Appraisal of taxonomic importance of some morphological characters

Our molecular data also suggest that some ascospore characters may be of less importance taxonomically than previously thought, for example, the "sand glass ascospores" with thick walls, which were used as a diagnostic character for *C. calcitrapa* (Navarro-Rosinés *et al*. 2000) and *C. dichroa* (Arup 2006*a*). In some specimens of both species, confirmed by molecular data, only thin-walled "*citrina*-type ascospores" were observed. This observation is particularly important taxonomically and further study of the phenomenon is planned.

We are grateful to André Aptroot for providing some herbarium material, Pavel Hrouzek (Třeboň, CZ) for analyzing the anthraquinones, Per Lassen (Lund) for providing Latin diagnoses and Jaroslav Šoun (České Budějovice) for his help with the molecular laboratory work. Our work was financially supported by the Grant Agency of the Academy of Sciences of the Czech Republic (KJB 601410701) and a grant from the European Commission's (FP 6) Integrated Infrastructure Initiative programme SYNTHESYS (DK-TAF).

References

Altekar, G., Dwarkadas, S., Huelsenbeck, J. P. & Ronquist, F. (2004). Parallel Metropolis-coupled Markov Chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* **20:** 407–415.

Aptroot, A. & van Herk, C. M. (2004) *Caloplaca britannica* common in non-maritime environments. *Lichenologist* **36:** 261–264.

Argüello, A., del Prado, R., Cubas, P. & Crespo, A. (2007) *Parmelia quercina* (*Parmeliaceae*, Lecanorales) includes four phylogenetically supported

morphospecies. *Biological Journal of the Linnean Society* **91:** 455–467.

Arnerup, J., Högberg, N. & Thor, G. (2004) Phylogenetic analysis of multiple loci reveal the population structure within *Letharia* in the Caucasus and Morocco. *Mycological Research* **108:** 311–316.

Arup, U. (1992*a*) *Caloplaca marina* and *C. rosei*, two difficult species in North America. *Bryologist* **95:** 148–160.

Arup, U. (1992*b*) *Caloplaca stantonii* sp. nov. and its relationship to *Caloplaca bolacina* and other lobate to squamulose species in North America. *Bryologist* **95:** 449–457.

Arup, U. (1993*a*) *Caloplaca flavogranulosa* sp. nov. and *C. citrina*, two sorediate species on seashore rocks in western North America. *Bryologist* **96:** 598–603.

Arup, U. (1993*b*) *Caloplaca luteominia* and *C. bolanderi* in western North America. *Bryologist* **96:** 463–470.

Arup, U. (1994) The genus *Caloplaca* on seashore rocks in eastern North America. *Bryologist* **97:** 377–392.

Arup, U. (1995*a*) Eight species of *Caloplaca* in coastal western North America. *Bryologist* **98:** 92–111.

Arup, U. (1995*b*) Littoral species of *Caloplaca* in North America: a summary and key. *Bryologist* **98:** 129–140.

Arup, U. (1997*a*) *Caloplaca maritima*, a misunderstood species in western Europe. *Lichenologist* **29:** 503–512.

Arup, U. (1997*b*) [1998] Correction of reports of two *Caloplaca* species from North America. *Bryologist* **100:** 516.

Arup, U. (2006*a*) A new taxonomy of the *Caloplaca citrina* group in the Nordic countries, except Iceland. *Lichenologist* **38:** 1–20.

Arup, U. (2006*b*) *Caloplaca sorediella* Arup, a new sorediate species from western Britain. *Lichenologist* **38:** 499–502.

Arup, U. (2006*c*) The status of *Caloplaca havaasii*. *Graphis Scripta* **18:** 33–37.

Arup, U. (2009) The *Caloplaca holocarpa* group in the Nordic countries, except Iceland. *Lichenologist* **41:** 111–130.

Arup, U., Arneng, E. & Søchting, U. (2007) *Caloplaca fuscorufa* – a misunderstood species in northern Europe. *Lichenologist* **39:** 409–414.

Arup, U. & Grube, M. (1999) Where does *Lecanora demissa* (Ascomycota, Lecanorales) belong? *Lichenologist* **31:** 419–430.

Brodo, I. M. & Santesson, R. (1997) Lichens of the Queen Charlotte Islands, British Columbia, Canada. 3. Marine species of *Verrucaria* (*Verrucariaceae*, Ascomycotina). *Journal of the Hattori Botanical Laboratory* **82:** 27–37.

Bungartz, F. (2002) Morphology and anatomy of the fertile structures. In *Lichen Flora of the Greater Sonoran Desert Region. I.* (T. H. Nash III, B. D. Ryan, C. Gries & F. Bungartz, eds): 24–35. Tempe: Lichens Unlimited, Arizona State University.

Crespo, A., Molina, M. C., Blanco, O., Schroeter, B., Sancho, L. G. & Hawksworth, D. L. (2002) rDNA ITS and -tubulin gene sequence analyses reveal two monophyletic groups within the cosmopolitan lichen *Parmelia saxatilis*. *Mycological Research* **106:** 788–795.

Ekman, S. (2001) Molecular phylogeny of the *Bacidiaceae* (Lecanorales, lichenized Ascomycota). *Mycological Research* **105:** 783–797.

Fletcher, A. (1973*a*) The ecology of marine (littoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5:** 368–400.

Fletcher, A. (1973*b*) The ecology of maritime (supralittoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5:** 401–422.

Fletcher, A. (1975*a*) Key for the identification of British marine and maritime lichens. I. Siliceous rocky shore species. *Lichenologist* **7:** 1–52.

Fletcher, A. (1975*b*) Key for the identification of British marine and maritime lichens. II. Calcareous and terricolous species. *Lichenologist* **7:** 73–115.

Foucard, T. (2001) *Svenska Skorplavar*. Stockholm: Interpublishing.

Gardes, M. & Bruns, T. D. (1993) ITS primers with enhanced specificity for basidiomycetes. Application for the identification of mycorrhizae and rusts. *Molecular Ecology* **2:** 113–118.

Gaya, E., Navarro-Rosinis, P., Llimona, X., Hladun, N. & Lutzoni, F. (2008) Phylogenetic reassessment of the Teloschistaceae (lichen-forming Ascomycota Lecanoromycetes). *Mycological Research* **112:** 528–546.

Güvenc, S. & Öztürk, S. (1999) Lichens in the northeast regions of Cyprus. *Feddes Repertorium* **110:** 455–463.

Hall, T. A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41:** 95–98.

Hansen, E. S., Poelt, J. & Søchting, U. (1987) Die Flechtengattung *Caloplaca* in Grønland. *Meddelelser om Grønland, Bioscience* **25:** 1–52.

Harada, H. (2004) Revision of marine and maritime species of *Verrucaria* in Japan. *Lichenology* **2:** 177.

John, V. & Breuss, O. (2004) Flechten der östlichen Schwarzmeer-Region in der Türkei (BLAM-Exkursion 1997) *Herzogia* **17:** 137–156.

Katoh, K., Kuma, K., Toh, H. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30:** 3059–3066.

Khodosovtsev, O. Y. (2001) [A new for Ukraine species of the genus *Caloplaca* Th. Fr. (Teloschistaceae).] *Ukrayinskyi Botanichnyi Zhurnal* **58:** 460–465 [in Ukrainian].

Khodosovtsev, O. Y. (2002) [A new for Ukraine and rare species of the genus *Caloplaca* Th. Fr. (Teloschistaceae) from southern Ukraine.] *Ukrayinskyi Botanichnyi Zhurnal* **59:** 321–329 [in Ukrainian].

Khodosovtsev, O. Y. (2003) [A new for Crimea and Ukraine species of lichens from siliceous outcrops.] *Ukrayinskyi Botanichnyi Zhurnal* **60:** 70–78 [in Ukrainian].

Khodosovtsev, O. Y., Kondratyuk, S. Y. & Kärnefelt, I. (2003): New species of *Caloplaca* from Crimean

Peninsula (Ukraine). *Ukrayinskyi Botanichnyi Zhurnal* **60:** 293–297.

Khodosovtsev, O. Y., Vondrák, J. & Šoun, J. (2007) New lichenized and lichenicolous fungi for the Crimean Peninsula (Ukraine). *Chornomorskyi Botanichnyi Zhurnal* **3:** 109–118.

Kroken, S. & Taylor, J. W. (2001) A gene genealogical approach to recognize phylogentic species boundaries in the lichenized fungus *Letharia*. *Mycologia* **93:** 38–53.

Laundon, J. R. (1992) New British species of *Caloplaca*. *Lichenologist* **24:** 1–5.

Laundon, J. R. (1976) Lichens new to the British flora: 5. *Lichenologist* **8:** 139–150.

Lindblom, L. & Ekman, S. (2005) Molecular evidence supports the distinction between *Xanthoria parietina* and *X. aureola* (Teloschistaceae, lichenized Ascomycota). *Mycological Research* **109:** 187–199.

McCarthy, P. M. (1991) Notes on Australian Verrucariaceae (Lichenes): 2. *Muelleria* **7:** 317–332.

Muggia, L., Grube, M. & Tretiach, M. (2008) A combined molecular and morphological approach to species delimitation in black-fruited, endolithic *Caloplaca*: high genetic and low morphological diversity. *Mycological Research* **112:** 36–49.

Navarro-Rosinés, P., Gaya, E. & Roux, C. (2000) *Caloplaca calcitrapa* sp. nov. (Teloschistaceae) un nuevo liquen saxícolo-calcícola mediterráneo. *Bulletin de la Société linnéenne de Provence* **51:** 145–152.

Navarro-Rosinés, P. & Hladun, N. L. (1996) Les especies saxícolo-calcícolas del grupo de *Caloplaca lactea* (Teloschistacceae, líquenes), en las regiones mediterranea y medioeuropea. *Bulletin de la Société linéenne de Provence* **47:** 139–166.

Navarro-Rosinés, P. & Roux, C. (1993) *Caloplaca tavaresiana* Nav.-Ros. et Roux sp. nov., espèce nouvelle de lichen du littoral de la région méditerranéenne. *Nova Hedwigia* **57:** 169–177.

Navarro-Rosinés, P. & Roux, C. (1995) *Caloplaca navasiana* Nav.-Ros. et Roux sp. nov., espèce nouvelle de lichen du littoral Méditerranéen. *Cryptogamie, Bryologie-Lichénologie* **16:** 89–97.

Nimis, P. L. & Poelt, J. (1987) The lichens and lichenicolous fungi of Sardinia (Italy): an annotated list. *Studia Geobotanica* **7:** 1–269.

Nimis, P. L., Poelt, J., Tretiach, M., Ottonello, D., Puntillo, D. & Vězda, A. (1994) Contributions to lichen floristics in Italy. VII – The lichens of Marettimo (Egadi Islands, Sicily). *Bulletin de la Société linnéenne de Provence* **45:** 247–262.

Nordin, I. (1972) Caloplaca *sect.* Gasparrinia *in Nordeuropa. Taxonomiska och Ekologiska Studier*. Uppsala: Skriv Service AB.

Nylander, J. A. A., Ronquist, F., Huelsenbeck, J. P. & Nieves-Aldrey, J. L. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology* **53:** 47–67.

Pišút, I. & Guttová, A. (2008) Contribution to the lichen flora of Anatolia, Turkey. *Sauteria* **15:** 403–416.

Redchenko, A. A. (2002) [The lichens of seaside part of Kerchen Peninsula.] *Ukrayinskyi Botanichnyi Zhurnal* **59:** 426–436 [in Ukrainian].

Ronquist, F. & Huelsenbeck, J. P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

Roux, C., Bricaud, O., Ménard, T., Gueidan, C., Coste, C. & Navarro-Rosinés, P. (2003) Champignons lichénisés et lichénicoles de la France méridionale (Corse comprise): espèces nouvelles et intéressantes (9). *Bulletin de la Société linnéenne de Provence* **54:** 125–141.

Roux, C. & Navarro-Rosinés, P. (1992) *Caloplaca egeana* Roux et Nav.-Ros. sp. nov. kaj *Caloplaca veneris* Roux et Nav.-Ros. sp. nov., du novaj likenspecioj de la mediteranea marbordo. *Bulletin de la Société linnéenne de Provence* **43:** 97–103.

Ryan, B. D., Bungartz, F. & Nash, T. H. III (2002) Morphology and anatomy of the lichen thallus. In *Lichen Flora of the Greater Sonoran Desert Region. I.* (T. H. Nash III, B. D. Ryan, C. Gries & F. Bungartz, eds): 8–23. Tempe: Lichens Unlimited, Arizona State University.

Sérusiaux, E., Diederich, P., Brand, A. M. & van den Boom, P. (1999) New or interesting lichens and lichenicolous fungi from Belgium and Luxembourg. VIII. *Lejeunia* **162:** 1–95.

Sheard, J. W. (1978) The taxonomy of the *Ramalina siliquosa* species aggregate (lichenized Ascomycetes). *Canadian Journal of Botany* **56:** 916–938.

Sipman, H. & Raus, T. (1999) A lichenological comparison of the Paros and Santorini island groups (Aegean, Greece), with annotated checklist. *Willdenowia* **29:** 239–297.

Sipman, H. & Raus, T. (2002) An inventory of the lichen flora of Kalimnos and parts of Kos (Dodecanisos, Greece). *Willdenowia* **32:** 351–392.

Sipman, H., Raus, T. & Scharlau, A. (2005) Some lichens have incomplete distribution ranges in the Aegean (Greece). *Folia Cryptogamica Estonica* **41:** 97–104.

Søchting, U. (1992) *Caloplaca soropelta* (E. S. Hansen, Poelt & Søchting) Søchting comb. nov. *Graphis Scripta* **4:** 35–36.

Søchting, U. (1997) Two major anthraquinone chemosyndromes in Teloschistaceae. *Bibliotheca Lichenologica* **68:** 135–144.

Søchting, U. & Figueras, G. (2007) *Caloplaca lenae* sp. nov., and other *Caloplaca* species with caloploicin and vicanicin. *Lichenologist* **39:** 7–14.

Søchting, U. & Lutzoni, F. (2003) Molecular phylogenetic study at the generic boundary between the lichen-forming fungi *Caloplaca* and *Xanthoria* (Ascomycota, *Teloschistaceae*). *Mycological Research* **107:** 1266–1276.

Swofford, D. L. (2002) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.* Sunderland, Massachusetts: Sinauer Associates.

Szatala, Ö. (1943*a*) Lichens. In K. H. Rechinger, Flora Aegaea – Flora der Inseln und Halbinseln des Ägäischen Meeres. *Denkschriften: Akademie*

der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Classe **105:** 16–58.

Szatala, Ö. (1943*b*) Lichenes. In K. H. Rechinger, Neue Beiträge zur Flora von Kreta (Ergebnisse einer biologischen Forschungsreise nach dem Peloponnes und nach Kreta 1942, im Auftrage des Oberkommandos der Wehrmacht und des Reichsforschungsrates, Nummer 6). *Denkschriften: Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Classe* **105**/(2): 27–47.

Tavares, C. N. (1956) Notes lichenologiques-IX. *Revista da Faculdade de Ciências de Lisboa. 2. ser. (C)* **5:** 123–134.

Tehler, A., Dahlkild, A., Eldenas, P. & Feige, G. B. (2004) The phylogeny and taxonomy of Macaronesian, European and Mediterranean *Roccella* (Roccellaceae, Arthoniales). *Symbolae Botanicae Upsalienses* **34**(1): 405–428.

Tretiach, M., Pinna, D. & Grube, M. (2003) *Caloplaca erodens* [sect. Pyrenodesmia]new species from Italy with an unusual thallus type. *Mycological Progress* **2:** 127–136.

Vězda, A. (1975) *Lichenes selecti exsiccati. Fasc. 55 (ns 1351-1375)*. Průhonice: Instituto Botanico Academiae Scientiarum Čechoslovacae.

Vězda, A. (1993) *Lichenes rariores exsiccati. Fasc. 6 (ns 51-60)*. Brno.

Vondrák, J. & Slavíková-Bayerová, Š. (2006) Contribution to the lichenized and lichenicolous fungi in Bulgaria. II, the genus *Caloplaca*. *Mycologica Balcanica* **3:** 61–69.

Vondrák, J., Kocourková, J., Palice, Z. & Liška, J. (2007) New and noteworthy lichens in the Czech Republic – genus *Caloplaca*. *Preslia* **79:** 163–184.

Vondrák, J., Guttová, A. & Mayrhofer, H. (2008*a*) A contribution to the knowledge of lichen-forming and lichenicolous fungi in Crete. *Herzogia* **21:** 105–124.

Vondrák, J., Khodosovtsev, A. & Říha, P. (2008*b*) *Caloplaca concreticola* (*Teloschistaceae*), a new species from anthropogenic substrata in Eastern Europe. *Lichenologist* **40:** 97–104.

Vondrák, J., Šoun, J., Hrouzek, P., Říha, P., Kubásek, J., Palice, Z. & Søchting, U. (2008*c*) *Caloplaca subalpina* and *C. thracopontica*, two new saxicolous species from the *Caloplaca cerina* group (*Teloschistales*). *Lichenologist* **40:** 375–386.

Wade, A. E. (1965) The genus *Caloplaca* Th. Fr. in the British Isles. *Lichenologist* **3:** 1–28.

Wetmore, C. M. (2003) The *Caloplaca squamulosa* group in North and Central America. *Bryologist* **106:** 147–156.

White, T. J., Bruns, T. D., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal DNA genes for phylogenies. In *PCR Protocols: a Guide to Methods and Applications* (M. A. Innis, D. H. Gelfand, J. J. Sninsky & T. J. White, eds): 315–322. San Diego: Academic Press.

Yazici, K. (1999) Trabzon ili likenleri [Lichen flora of Trabzon]. *Turkish Journal of Botany* **23:** 97–112 [in Turkish].

Accepted for publication 30 *March* 2009